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PhD Thesis

**A COMPARATIVE STUDY OF FRONTAL BONE
MORPHOLOGY OF LATE PLEISTOCENE FOSSIL HOMININS
FROM THE TERRITORY OF THE FORMER SOVIET UNION**

Submitted by Ekaterina Bulygina

Supervised by Dr. Charles Lockwood and

by Prof. Leslie Aiello

University College London

2007

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Abstract

The major aim of the present work is to provide a re-assessment of the morphological and taxonomic affinities of several adult and juvenile fossils from the territory of the former Soviet Union that retain frontal bones. Nine fossils were analysed and compared with a sample of Late Pleistocene hominins and recent modern populations. Analytical techniques included traditional inter-landmark measurements, as well as a geometric morphometric toolkit for the 3D surfaces. The following patterns were found in the comparative sample: 1) the best differentiation in the frontal bone morphology exists between the 'modern' and 'archaic' groups of hominins, where the former is composed of recent and Upper Palaeolithic modern humans, and the latter incorporates Neanderthals and early modern humans from Africa and West Asia; 2) Upper Palaeolithic humans from central and eastern Europe differ significantly from the pooled sample of the nine recent modern human populations; 3) the morphology of the complete frontal bone discriminates between hominin groups better than the supraorbital relief; 4) recent modern humans and Neanderthals display diverging growth trajectories in the shape of the frontal bone; differences already exist at the earliest age stages represented here (2.5 years in Neanderthals) and increase towards adulthood.

Within the above framework, all Sungir' fossils align with the recent modern human morphological variation. In contrast, the fossil frontal from Podkumok, North Caucasus, is associated with the Upper Palaeolithic sample of fossils. Satanay, Khvalynsk and Skhodnya frontal bones have an ambiguous morphological associations generally aligning with the modern morphology but demonstrating particular combination of features that sometimes

make them closer to the 'archaic' fossils in the sample. The Teshik-Tash child is found to be similar to Neanderthals in the frontal bone morphology. However, it shows lesser degree of the development of the 'classical' Neanderthal morphology and deviates towards the early modern humans. The Starosel'e child did not demonstrate any affiliation with the 'archaic' morphological pattern in its frontal bone.

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Chapter 1 Introduction

According to archaeological evidence, the history of hominin settlement of north-eastern Eurasia, i.e. former Soviet Union, does not exactly conform to the models developed on the basis of the western and central European record. It has been demonstrated that Middle Palaeolithic Mousterian cultural traditions persisted here well into the time period represented by Upper Palaeolithic elsewhere (Bradley et al., 1995; Pavlov et al., 2004; Sinitsyn et al., 1997b). Moreover, there is reason to believe that not all Middle Palaeolithic cultural assemblages were made by Neanderthals, whereas all the 'Transitional' cultures here were the handiwork of the early modern humans (see below). Unfortunately, the palaeoanthropological record from this territory is not very rich. Nevertheless, the known Late Pleistocene remains of hominins have been assigned to both Neanderthals and modern humans and there is evidence of late survival of Neanderthals in the south of the area overlapping in time with modern humans here (see below).

Until relatively recently, Russian palaeoanthropologists were greatly influenced by the school of Schwalbe (1904; 1902; 1906), Gorjanović-Kramberger (1906) and Hrdlička (1930), who believed that Neanderthals represent a logical ancestor of modern humans. This is reflected in the development of the idea of 'Broad Monocentrism' (Roginski, 1947a; 1947b; 1949; 1951; 1977; Alexeev, 1974; 1978; Debets, 1950) where Neanderthals were seen as a stage in the development of modern humans. Kozinstev (1990; 1994; 1997; 1999; 2003) re-formulated this idea in the light of the recent discoveries in genetics, archaeology and palaeoanthropology. He argued for the presence of the Neanderthal heritage of some morphological characteristics in modern humans in Europe that is especially pronounced in

early Anatomically Modern Humans (AMH) from marginal areas of Neanderthal dispersal. In this later version, 'Broad Monocentrism' becomes more similar to the 'Assimilation model' proposed by Smith *et al.* (1989a) (see also Smith *et al.*, 2005; Trinkaus, 2005).

As a result of this tradition, a number of fossils discovered in Russia and the Soviet Union during the course of the last century were assessed for the presence of 'archaic' traits that frequently meant Neanderthal heritage. For instance, Gremyatski (1922; 1934; 1948; 1952a; 1952b) describes the morphology of frontal bones from Skhodnya, Podkumok and Khvalynsk as 'Transitional' following the description of crania from Brx, Slovak Republic, and Cannstadt, Central Europe, by Schwalbe (1906). A child from a Mousterian layer at Starosel'e, Crimea, although found to be a modern human, has been attributed a number of 'archaic' traits, such as considerable thickness of the zygomatic processes of the frontal bone, large teeth, a great width of the anterior section of the mandible, and relatively flat frontal and parietals (Roginski, 1954; see also review in Alexeev, 1976). The association of the modern child with Mousterian artefacts was used to argue that morphological evolution preceded cultural (Roginski, 1954). On the other hand, the Neanderthal child from Teshik-Tash has been noted to express a number of Neanderthal cranial and postcranial features to a lesser extent than expected, which could either be a function of the individual's young age or represent the 'Transitional' morphology (Sinelnikov and Gremyatski, 1949; Gremyatski, 1949).

In the light of the current development of the argument on the Neanderthal legacy in modern humans, a new study of the fossils from the north-eastern Eurasia is required. A tendency to re-assess the old work of Soviet palaeoanthropologists has recently been demonstrated in a monograph dedicated to Sungir' findings (Alexeeva *et al.*, 2000).

However, this work has been criticised for swinging the pendulum in the opposite direction by rejecting former comparative anatomical results on weak grounds (Kosintsev, 2003). Researchers outside Russia have also criticised the phylogenetic and cultural affiliations of some of the fossils from north-eastern Eurasia. For example, Marks *et al.* (1997) claimed that the Starosel'e child is a modern individual that was not actually associated with the Mousterian layer at all but was coming from an intrusive burial from an overlying Holocene horizon. Glants and Ritzman (2004) and Ritzman (2005) concluded that Teshik-Tash is not a Neanderthal on the basis of discriminant analysis of cranial features contrary to Gremyatski (1949).

Frontal bones are relatively well represented in the fossil material from north-eastern Eurasia either as separate fossils or parts of more complete crania. The major aim of the present work is a re-assessment of morphological affinities of several Late Pleistocene fossils from the territory of north-eastern Eurasia, including both adult and juvenile individuals that retain frontal bones. They are compared with broadly contemporaneous fossils from Europe and western Asia as well as with modern human populations by means of traditional and geometric morphometric methods.

The comparative analysis is performed in several steps. First, the traditional inter-landmark measurements of the North-East Eurasian individuals and the comparative sample are analysed together using multivariate statistics. The adult sample of individuals is considered first followed by the analysis of the full, 'ontogenetic' sample including children and sub-adults. Secondly, the complete surface of the frontal bone is analysed using geometric morphometric methods for 3D surfaces. As in the previous step, adults and the full ontogenetic sample of individuals are considered separately. For both 3D and

traditional analyses, conclusions are drawn regarding the pattern of morphological affinities within the whole comparative sample and for the affinities of the North-East Eurasian fossils in particular. The results of the traditional analysis of inter-landmark distances are compared with the results of the 3D analysis of the complete frontal bone surface. In addition, special attention is given to the problem of missing data reconstruction for inter-landmark distances and for 3D surfaces.

Chapter 2 Literature Review

Early modern humans in Europe and the Neanderthal legacy

The past decade has seen a continuous flow of work contribute to our knowledge of the history of early modern humans and Neanderthals. New information comes from discoveries, such as the Herto skull in Ethiopia and the site of Peșcera cu Oase in Romania, a wave of direct dating of well-known fossils, archaeological data, genetic research and morphological analyses. Such research fuels the long-standing debate on the origin of modern humans and the fate of Neanderthals. Klein (2003) suggests that given all the accumulated information, ‘the longest continuous debate in palaeoanthropology is nearing its resolution... modern humans replaced Neanderthals with little or no gene exchange’. On the other hand, recent publications demonstrate that the proponents of the three major hypotheses on the origin of modern humans maintain their distinct positions in the face of new discoveries (Stringer, 2002a; 2002b; Smith et al., 2005; Trinkaus, 2005; 2006b; Wolpoff et al., 2004; 2005).

The three major hypotheses are divided on the place of origin of modern humanity and the amount of genetic contribution that local populations made to the modern gene pool. The first model, known as ‘Replacement’, ‘Single Origin’ or ‘Out-of-Africa’ (Howells, 1976; Hublin and Tiller, 1992; Stringer, 1992a; 1992b) argues for the independent origin of modern humans in Africa with subsequent migrations and replacement of indigenous populations. The model either totally excludes genetic exchange between the modern incomers and aboriginal archaic populations (see, for example, Currat and Excoffier, 2004)

or allows for insignificant hybridization between them (Stringer and Bräuer, 1994; Bräuer and Stringer, 1997; Bräuer and Broeg, 1998; Klein, 1999; Bräuer, 2001). The second hypothesis, proposed by Smith *et al.* (1989a) and known as the ‘Assimilation model’, agrees on the African origin and dispersal of modern humans but argues that interbreeding between the newcomers and local populations was neither accidental nor trivial (Smith *et al.*, 2005; Trinkaus, 2005). The third model assumes regional continuity without any major population migrations out of Africa but the movement of genes through population exchange (Wolpoff, 1989b; 1989c).

An African root of modern human genetic diversity is supported by the majority of genetic research on mitochondrial DNA (Cann *et al.*, 1987; Vigilant *et al.*, 1991; Ingman *et al.*, 2000; Maca-Meyer *et al.*, 2001; Takahata *et al.*, 2001; Macaulay *et al.*, 2005; see also reviews in Relethford, 2001; and Torroni *et al.*, 2006), Y-chromosome polymorphisms (Hammer *et al.*, 1998; 2001; 2003; Underhill *et al.*, 2000; 2001; Agrawal *et al.*, 2005), X-chromosome-linked polymorphisms (Harris and Hey, 1999; Kaessmann *et al.*, 1999; Alonso and Armour, 2004) and a few autosomal polymorphisms and microsatellite markers in recent human populations (Harding *et al.*, 1997; Jin *et al.*, 1999; Rana *et al.*, 1999; Rogers *et al.*, 2000; Zhang and Rosenberg, 2000; Ma *et al.*, 2002). However, analyses of the genetic data disagree on the amount of admixture between expanding modern humans and local populations, ranging from the complete absence of admixture between early modern humans and Neanderthals in Europe (Currat and Excoffier, 2004) to the strong support of interbreeding, not replacement, during at least two major expansions after the original *Homo erectus* range extension out of Africa (Templeton, 2002; 2005) or wave-like demic diffusion of an advantageous modern phenotype (Eswaran, 2002; 2005). It is

generally maintained that the present data do not allow ruling out some degree of admixture between the expanding modern humans and some ancient local populations (Nordborg, 1998; 2000; Harpending and Rogers, 2000; Wall, 2000; Eswaran, 2002; 2005; Tishkoff and Verrelli, 2003; Harpending and Eswaran, 2005).

A number of studies on ancient mitochondrial DNA in Neanderthals and Aurignacian and Gravettian – associated early modern humans in Europe (Krings et al., 1997; 1999; 2000; Ovchinnikov et al., 2000; Scholz et al., 2000; Schmitz et al., 2002; Caramelli et al., 2003) corroborate the replacement model due to the pronounced differences between Neanderthal and recent human mitochondrial DNA and the absence of any traces of Neanderthal signature in the mitochondrial DNA of either recent or early modern humans. This conclusion has been criticized on the grounds that it does not take into account the whole range of possible scenarios of population history that could ultimately result in the disappearance of the Neanderthal signature in the modern mitochondrial DNA pool due to genetic drift (Nordborg, 1998; Relethford 2001; Serre *et al.*, 2004). Nordborg (1998) and Relethford (2001) stress that further genetic extraction of Neanderthal mitochondrial DNA is unlikely to resolve this issue.

Weaver and Roseman (2005) reviewed and re-analysed evidence from the mitochondrial DNA recovered from Neanderthal fossils by modelling population history. They concluded that, if the archaeological evidence for the long survival of Neanderthals in Europe is taken into account, their per-generation contribution to the early modern human population must have been fairly small (less than 0.2%) or we would find Neanderthal mitochondrial DNA lineages in living humans. If the human population size remained constant and small until very recently, then the total accumulated Neanderthal admixture could still have been large,

but if the human population started to grow rapidly from a small size about 40,000 years ago, then even a very small Neanderthal genetic contribution to modern human populations can be ruled out. The current evidence on the modern human population size in the Late Pleistocene is controversial and largely dependent on the genetic region and type of the marker analysed as well as bias control in the sample (Weaver and Roseman, 2005). Thus, mitochondrial DNA appears to show a rapid population growth between 200,000 and 40,000 years ago (Excoffier 2002, Excoffier and Schneider 1999; Harpending et al, 1998, Ingman et al, 2000). However, other authors suggest that the same pattern of distribution of the mtDNA polymorphism could have resulted from a selective sweep (Hawks et al, 2000, Hawks and Wolpoff, 2001; Hey, 1997, Wise et al., 1998).

Results of analyses of nuclear genome-wide microsatellites corroborate the population expansion found in mtDNA polymorphisms (Pitchard et al., 1999; Zhivotovski et al, 2003), whereas autosomal and X-chromosome coding sequences and single nucleotide polymorphisms (SNPs) tend to show either no evidence of expansion or are equivocal (Harris and Hey, 1999; Harpending and Rogers, 2000; Ptak and Przeworski, 2002; Wall and Przeworski, 2000). A study of the genome-wide SNPs by Marth et al. (2004) was the first work to provide for a support of the fast population expansion by this type of genetic marker. On the whole, Weaver and Roseman (2005) argue that the signal of expansion provided by a number of genome-wide genetic systems agrees with the archaeological evidence of the fast human expansion (Klein *et al.*, 2004; Stiner *et al.*, 1999) and is in agreement with the scenario when many loci must have undergone increase in variation with the population expansion event as opposed to the selective sweep, which should have resulted in only few linked loci expressing this pattern (Weaver and Roseman, 2005).

Archaeological evidence for the fate of Neanderthals and early modern humans in Europe has also been a recent battle ground. Mellars (1996; 2004; 2005) , and Klein (1999) support a hypothesis under which modern human expansion across Europe is marked by the appearance of a highly uniform Aurignacian archaeological culture at about 40,000–35,000 years BP. The speed of such an expansion could have been relatively fast, similar to the later expansion of Neolithic farmers, as it has recently been demonstrated by new dates of a number of key sites (Bronk Ramsey et al., 2004; Mellars, 2006). It must have taken about 5,000 years between 46,000 and 41,000 years for the modern Upper Palaeolithic technological cultures to expand from the Levant to western Europe (Mellars, 2006). This expansion was characterised by abundant expression of abstract and artistic cognitive activities, among other features. These are reflected in the first complex and carefully shaped bone, antler and ivory tools, a sudden proliferation of perforated animal teeth, far-travelled marine shells, carefully shaped stone and ivory beads and other forms of personal ornaments and varied and sophisticated forms of abstract and figurative art, such as engravings, figurines and cave paintings (Mellars, 2004). In these characteristics, the Aurignacian contrasts with the Mousterian culture of the Middle Palaeolithic, which has been undoubtedly attributed to Neanderthals at least in Europe (Churchill and Smith, 2000b; Gamble, 1986; Klein, 1999; Mellars, 1996).

According to this view, the Aurignacian must have evolved somewhere outside Europe, possibly in western Asia, and there may be some traces of its initial development in Africa. Mellars (2004, 2005) points out discoveries in Howiesons Poort levels at Klasies River Mouth in South Africa, dated to around 70,000 years BP (Deacon, 1989; 2000; Deacon and Deacon, 1999; Singer and Wymer, 1982) and Still Bay levels at the nearby Blombos Cave

dated to ca. 80,000-25,000 years BP (Henshilwood et al., 2001b; Henshilwood et al., 2001a; Henshilwood et al., 2002; Henshilwood et al., 2004) as examples of the first appearance of explicitly Upper Palaeolithic technologies, extensive red ochre use and a range of 'artistic' or 'decorative' items such as pieces of red ochre with incised criss-cross design motifs and a large number of carefully perforated seashells.

Archaeological inferences about the early modern human expansion routes out of Africa have recently received a new spin from the research on mtDNA variation in East Asian populations (Ingman et al., 2000; Macaulay et al., 2005; Thangaraj et al., 2005; see also Forster, 2004). This research showed evidence of a single human expansion event out of Africa sometime between 80,000 and 60,000 years BP along the coastal route of the Indian Ocean Littoral. According to this scenario, the early settlement of western Eurasia must have represented an early off-shoot of this expansion. Mellars (2006) discusses the archaeological data available from the sites along the southern coastal route and the data from the western Eurasia and concludes that there is substantial material support for this hypothesis.

The above scenario seems logical but for a few questions about the precise relationship between different hominin species and the Middle and Upper Palaeolithic technologies outlined above. First of all, the archaic modern humans from western Asia, such as Skhul and Qafzeh, are found in association with Mousterian artefacts (McCown and Keith, 1939; Vandermeersch, 1989) as are their Neanderthal counterparts from the same area. The majority of Neanderthal finds from western Asia are dated later than Skhul and Qafzeh hominins. Thus, the Kebara Neanderthals in Israel come from a layer that was dated to about 60,000 years BP by thermoluminescence (TL) and electron spin resonance (ESR)

methods (Valladas et al., 1987; Bar-Yosef, 1992) . The Amud Neanderthals also in Israel showed a TL date of 45,000–47,000 years BP (Suzuki and Takai, 1970; Rak et al., 1994). Shanidar, Iraq, yielded two groups of Neanderthals, dated to 60,000 and 46,000 years BP respectively (Trinkaus, 1983; 1991; Bar-Yosef, 1992). The latest available dates for bone samples from Skhul, Tabun C1 and Qafzeh show that these fossils are broadly contemporaneous falling within the time range of 100,000 to 130,000 years BP (Grün and Stringer, 1991; Mercier et al., 1993; Mercier et al., 1995; Yokoyama et al., 1997; Schwarcz et al., 1998; Grün and Stringer, 2000; Mercier and Valladas, 2003; Grün et al., 2005). Therefore, early representatives of both early modern humans and Neanderthals were present in Levant during Oxygen Isotope Stage (OIS) 5, which ‘...inevitably complicates attempts at segregating these populations by date or archaeological association’ (Grün et al., 2005, p. 332). The Skhul and Qafzeh finds are frequently interpreted as a brief expansion of anatomically modern populations from Africa to the adjacent parts of western Asia at an early stage in the last glaciations (Lahr and Foley, 1998; Bar-Yosef, 2000; Stringer, 2002a; Trinkaus, 2005) but there is no unequivocal conclusion.

The complications do not stop here. The Upper Palaeolithic complexes that appear to have technological and typological connections to the Mousterian - Chatelperronian, Uluzzian and Szeletian - have uncertain relationships to the makers of the Aurignacian culture (Churchill and Smith, 2000b). It is now clear that Chatelperronian was a product of Neanderthals, as shown by association with Neanderthal remains at St. Césaire and Arcy-sur-Cure in France (Leveque and Vandermeersch, 1980; Hublin et al., 1996; Trinkaus et al., 1999). In their analysis of early Upper Palaeolithic cultures of Europe, Zilhão and d’Errico (Zilhão and D’Errico, 2000b) imply that Uluzzian in central Europe and Szeletian in Italy

could be products of Neanderthals following the example of Chatelperronian in France. However, the majority of known remains associated with either of the former are mostly teeth that have been demonstrated morphologically inconclusive (Churchill and Smith, 2000). One recent report by Ahern *et al.* (2004) on new findings of Neanderthal fossils from Vindija, Croatia, might confirm a Neanderthal association with early Upper Palaeolithic cultures in Eastern Europe. According to Ahern *et al.* (2004), one of the postcranial remains, a radius fragment that comes from level G(1), exhibits Neanderthal-like anatomy and is congruent with the previously established association of Neanderthals with an early Upper Palaeolithic industry at the site.

Trinkaus (2005) draws attention to another problem whereby the European early modern human sample size has been reduced due to the recent cleansing of the early Upper Palaeolithic human fossil record. Thus, the Cro-Magnon fossils were re-dated to early Gravettian (27,760 radiocarbon years BP) (see Henry-Gambier, 2002; Conard *et al.*, 2004). The Zlatý kůň partial skeleton, formerly attributed to early Upper Palaeolithic, and tentatively associated with some form of the Upper Palaeolithic industry (see review in Churchill and Smith, 2000), recently was given ^{14}C Accelerator Mass Spectrometry (AMS) 12,870 \pm 70 years (in uncalibrated radiocarbon years) (Svoboda *et al.*, 2002). The frontal bone Hahnöfersand 1, Germany, previously thought to date to 36,000 years BP, was dated to 7,500 \pm 55 radiocarbon years BP by Terberger *et al.* (2001). The same fate befell human remains from St. Prokop, Velica Pečina and Vogelherd that were formerly early Upper Palaeolithic (i.e. 34,000–32,000 years BP) and now Holocene (Svoboda *et al.*, 2004; Smith *et al.*, 1999; Conard *et al.*, 2004 respectively). Therefore, the early Aurignacian in Europe is no more firmly associated with the modern human remains.

Mellars (2004, 2005) stresses that a number of fossil remains of the early modern humans, such as Peșcera cu Oase in Romania, Ksar Akil in Levant, Kent's Cavern in England, Mladeč in the Czech Republic and mandibles from Les Rois in France, are dated within the same time span as the conventional Middle–Upper Palaeolithic transition in Europe. Les Rois and Ksar Akil are apparently firmly associated with an Aurignacian Upper Palaeolithic technology (Mellars, 2005). Therefore, it would be an 'impossible coincidence' if the new rapidly-expanding Aurignacian culture was not connected with the new expanding modern human population in Europe, given that Neanderthals maintained typically Middle Palaeolithic technology and behaviour all through the previous 200,000 years (Mellars, 2005).

Mellars (1996, 2004, 2005) develops the idea of 'acculturation' of Neanderthals by expanding modern humans implying either coexistence of the two populations over some period in Europe or 'travel of ideas' ahead of humans through population contacts. This hypothesis has been criticized by d'Errico *et al.* (1998) and Zilhão and d'Errico (1999; 2000a). These authors come to the conclusion that true Aurignacian cannot be detected in Europe before 36,500 years BP, whereas Chatelperronian sites mostly pre-date 38,000 years BP. Therefore, Neanderthals must have accomplished their own Middle-to-Upper Palaeolithic transition by the time the first Aurignacian modern humans arrived.

The argument presented by d'Errico *et al.* (1998) and Zilhão and d'Errico (1999; 2000a) implies that there is no evidence of coexistence of Neanderthals and Upper Palaeolithic modern humans before 36,000 years BP. However, one report by Gravina *et al.* (2005) on new AMS dates for sequence of late Neanderthal and early anatomically modern occupational levels at the Grotte des Fees de Chatelperron, in east-central France, implies

interstratifications of Neanderthal and modern human occupational horizons and therefore the possibility of their co-existence. In other words, the question of the cultural contacts between modern humans and Neanderthals is still a debated area of archaeological research.

The hypothesis of the Aurignacian expansion of modern humans implies an extra-European origin of this culture. Unlike Mellars (2004, 2005), Smith (2005) finds the evidence of the putative precursor of the true Aurignacian outside Europe unconvincing (following reviews in Straus, 1995; 1997; 2003; Clark, 1997; Karavanic and Smith, 1998; Churchill and Smith, 2000a). Smith (2005) supports the results of the analysis by Kozłowski and Otte (2000) who believe that Aurignacian was not as uniform as it is often suggested. Kozłowski and Otte (2000) maintain that local manifestations of the Aurignacian culture are characterized by varying degrees of assimilation of local Middle Palaeolithic influences, as is especially clear from eastern and central European early Upper Palaeolithic assemblages. In addition, Upper Palaeolithic cultures that pre-date Aurignacian in the Levant (Initial Upper Palaeolithic and Ahmarian) (Kozłowski, 2005) and Streletskaya culture from the Russian Plain (Bradley et al., 1995; Sinitsyn et al., 1997b; Sinitsyn, 2003; Pavlov et al., 2004) show some unmistakably Middle Palaeolithic aspects of technology. Makers of the Levantine pre-Aurignacian cultures are not known. For the Russian plain, it is argued that traces of no other hominins apart from Anatomically Modern Humans have been detected in association with Streletskayan culture to date (Bradley et al., 1995; Sinitsyn et al., 1997b; Sinitsyn, 2003; Dolukhanov et al., 2001; 2002).

The inconclusiveness of the genetic and archaeological data allows for arguments of multiregional and assimilation models. Wolpoff *et al.* (2004), in their reply to Klein (2003),

argue that the hypothesis that Neanderthals are a significant part of the ancestry of Europeans is well supported and that the evidence from the skeletal anatomy, mitochondrial DNA, morphology and genetics of speech and the archaeology of the Middle–Upper Palaeolithic transition in Europe directly contradicts all elements of the replacement scenario. Their argument from the skeletal anatomy point of view is presented below.

The multiregional model argument of Wolpoff *et al.* (2004) essentially merges with the assimilation model in their statement that Neanderthals were not the unique ancestors of the later Europeans but rather, "...provided enough of a genetic contribution for their traits to be readily identifiable in later Europeans and ... even found in Europeans today" (Wolpoff *et al.*, 2004 p. 528). Among the latter skeletal features, Wolpoff *et al.* (2004), point out: 1) the high nasal angle involving the slope of the lofty nasal bridge, as it rises up between the orbits, incorporating the frontal process of the maxillae as well as the nasal bones themselves; 2) the course of the zygomaxillary suture (turning inward at its inferior aspect); 3) the maxillary expansion at the lateral nasal borders; and 4) the lateral zygomatic orientation. According to Wolpoff *et al.* (2004), these features are not present in Neanderthal contemporaries that are deemed to be among the closest ancestors of modern humans in Europe such as those from Qafzeh in Western Asia or the Herto skull from Ethiopia. Wolpff *et al.* (2004) argue that although these features are not autapomorphic for Europeans, their frequency in Europe is higher than anywhere else in the world, and they link fossil and modern European populations through time. Moreover, the above authors stress that a number of supposedly unique Neanderthal features, such as retromolar space, posterior placement of the mandibular mental foramen, taurodontism, the lateral (in contrast to superior) frontal sinus conformations, mastoid tubercle, suprainiac fossa,

lambdoidal flattening, H-O mandibular foramen, dorsal axillary border configuration of the scapula all show considerable variation within Neanderthals and a continuous distribution from Mousterian to early Upper Palaeolithic populations (Gorjanovic'-Kramberger, 1906; Weidenreich, 1943a; Smith, 1987; Wolpoff, 1989a; Caspari, 1991; Frayer, 1992; Franciscus and Trinkaus, 1995; Churchill, 1996). Given a very poor record of early post-Neanderthal Europeans, Wolpoff *et al.* (2004) underline the extraordinary fact of even finding these features in the small sample of early modern fossils known to date. For example, as was shown by Wolpoff (1989c), the Mladeč males have sagittal dimensions and profiles that deviate far less from the Neanderthals than they deviate from the Skhul/Qafzeh males. In addition, Mladeč 5 has a well-developed occipitomastoid crest, minimal mastoid projection and evidence of midfacial prognatism. Mladeč 6 has a suprainiac fossa of elliptical form, extensive lambdoidal flattening and a short posterior face on its occipital. Mladeč 8 has an exceptionally large maxillary canine and a groove along the inferior nasal margin and the remnant of a medial projection on the internal wall of the nasal aperture. Wolpoff *et al.* (2004) suggest that the real break in the majority of the 'Neanderthal' autapomorphies in the European population occurs between the Aurignacian and the Magdalenian/Mesolithic populations followed by further loss of remaining ancient genes during the population replacement at the onset of the Neolithic (following Chikhi *et al.*, 1998; 2002; Dupanloup *et al.*, 2004).

The second line of the argument in Wolpoff *et al.* (2004) is related to the claim that a number of Neanderthal autapomorphic features vary in their expression in Neanderthals and other hominins and some show temporal clines. For instance they refer to the report by Ponce de Leon and Zollikofer (1999) on absence of the distinctive Neanderthal alignment

of the bony labyrinth in the inner ear (Hublin et al., 1996) of the Le Moustier Neanderthal. Also, it seems that the distinctive Neanderthal nasal features described by Schwartz and Tattersall (1996) occur in modern humans, not only in the Neanderthals (Wolpoff and Frayer, 2005). A number of features of the Neanderthal mandibular ramus, previously described as autapomorphic (Rak, 1998), in fact regularly appear in populations predating and postdating Neanderthals (Wolpoff and Frayer, 2005). Moreover, later Neanderthals demonstrate higher foreheads, development of chins, reduction of facial prognatism and browridge dimensions suggesting a trend to emergence of 'modern' features over time (Wolpoff, 1989b; Frayer, 1997; Rak, 1998; Ahern et al., 2002). In summary, Wolpoff *et al.* (2004) do not see reason why Neanderthals should be excluded from the European ancestry, given the morphological evidence presented and inconclusiveness of other lines of research.

Smith *et al.* (2005) agree that traces of admixture between Neanderthals and early modern humans are found in anatomical detail, even though basic 'gestalt' of the cranial form is different between these two groups of hominins (Stringer and Andrews, 1988; Bräuer, 1984; 1989; Lahr, 1994; 1997; Turbon et al., 1997; Bräuer and Broeg, 1998; Harvati et al., 2004). Smith (2005) discusses the presence of high nasion projection from the bi-*frontomalaretemporale* line (Frayer, 1992), suprainiac fossa and occipital buns in European, African and west Asian Pleistocene fossils. He comes to the conclusion that the most logical explanation of the higher incidence of these features in early modern humans in Europe is their inheritance from Neanderthals, especially given that the Skhul and Qafzeh populations, the putative ancestors for the former, lack any of them.

Trinkaus (2005) presents a review of the fossil evidence following the recent decimation of the record by direct dating of the Late Pleistocene fossils. He supports the African origin of modern humanity but argues that early modern Eurasians exhibited a combination of distinctively modern morphologies with a "... variably present suite of archaic human features", which "...made them 'modern' without being fully modern" (Trinkaus, 2005, p.218). Among these archaic features are low temporal squamous profile, prominent juxtamastoid eminences, broad interorbital breadths, large dental arcades, exceptionally large third molars, broad mandibular rami, mandibular corpus robusticity, and variable maxillary incisor shovelling. According to Trinkaus (2005), the fossils from Dar-es-Soltane and Temara in Morocco, Nazlet Khater in Egypt, Cioclovina, Muierii and Oase in Romania, Mladeč in Czech Republic and Les Rois in France carry a combination of these archaic features with the modern general 'gestalt' of the cranium. These morphological attributes are generally present among late archaic humans as well as in Neanderthals, but already absent from the Qafzeh and Skhul remains (Trinkaus, 2005). The unilateral bridging of the mandibular foramen in Oase 1 is one distinctively Neanderthal feature that appears in the sample of the early modern humans in Europe. The considerably richer post-28,000 years BP Gravettian sample of early modern human fossils in Europe mostly have a fully modern morphology. However, Zilhão and Trinkaus (2002) and Trinkaus (2005) argue for the Neanderthal rather than tropical modern human proportions in the postcranial skeleton of the child from Lagar Vehlo in Portugal. According to these authors the occurrence of such arguably Neanderthal features, however rare it is in the Gravettian modern humans, points to their Neanderthal heritage in the Upper Palaeolithic European population. Trinkaus (2005), therefore, supports the Assimilation model.

The morphological support for the Replacement model comes from a number of multivariate analyses that quantify either the ‘basic gestalt’ of the cranial morphology (Howells, 1973; 1989; Stringer and Andrews, 1988; Bräuer, 1984; 1989; Stringer, 1992b; Lahr, 1994; 1997; Turbon et al., 1997; Bräuer and Broeg, 1998; Harvati et al., 2004) or discrete features initially proposed as evidence for regional continuity (Bräuer and Broeg, 1998; Lahr, 1996). The uniform message of these analyses is the evidence of great differences in cranial morphology of Neanderthals compared to recent and Upper Palaeolithic modern humans. No regional continuity of features, as implied by Multiregional and Assimilation models are detected (Bräuer and Broeg, 1998; Lahr, 1996).

Harvati *et al.* (2004) use new methods of three-dimensional geometric morphometrics to compare the degree of the Neanderthal morphological differentiation from modern humans to that found within and between 12 species of extant primates. On the basis of calculated morphological distances between model taxon pairs and distances between Neanderthals and modern humans Harvati *et al.* (2004) find that the result strongly supports a specific distinction for Neanderthals and the lack of a morphological signal of interbreeding between early modern human and Neanderthals. This argument is however weakened by the small sample of Neanderthals and early modern humans involved in the study.

Unfortunately, a similar study of general cranial shape that would include the majority of the key specimens from eastern and central Europe together with other west European Neanderthals and early modern human specimens might not be feasible due to the fragmentary nature of the fossil data.

Harvati (2003) and Gunz and Harvati (2006) address the question of morphological differences between Neanderthals and modern humans regarding separate cranial regions,

e.g. temporal and occipital bones, respectively. According to Harvati (2003), the 3D morphology of the temporal bone successfully separates Neanderthals from modern humans. The occipital morphology, however, does not provide for an absolutely clear-cut answer: the analysis of the midsagittal outline of the occipital shows almost complete overlap of Neanderthals' and modern humans' shape variability, whereas when midsagittal outline is augmented by the lambdoidal suture curve, Neanderthals fall outside the range of modern variation.

This result mirrors a polarization of the opinions on the presence and homology of the occipital bun features in Neanderthals, early modern humans and archaic modern humans from Levant. Whereas a number of authors see the occipital bun as continuous in Neanderthals and early modern humans (Wolpoff et al., 2001; 2004; Smith et al., 2005), others stress differences between Neanderthals and the early modern human condition that is found, for example, in Mladeč 6. In detail, the Neanderthal occipital features include extensive lambdoidal flattening, more acute angulation between the nuchal plane and the general orientation of the occipital plane, and the laterally wider bun (Smith, 1984; Trinkaus and LeMay, 1982; Caspari, 1991; Churchill and Smith, 2000b; Smith et al., 2005; Wolpoff et al., 2001; 2004; see review in Bräuer et al., 2004). The occipital bun in early modern humans has been described as restricted to the central portion of the occipital and labelled a 'hemibun' (Smith, 1984). Lieberman *et al.* (2000a), however, argued that early modern occipital morphology may be not homologous to Neanderthals' bun.

Moreover, the issue of the identification of lambdoidal flattening and occipital bunning seems to be highly subjective. For instance, Frayer (Frayer, 1992), Smith *et al.* (1995) and Smith *et al.* (2005) find that specimens from Skhul and Qafzeh lack development of either

lambdoidal flattening or occipital buns whereas Mladeč 5 and 6 have structures at least similar to the occipital buns, i.e. 'hemibuns'. In contrast, Bräuer (2003, cited by Bräuer et al. 2004) demonstrates that the parieto-occipital contours of Levantine fossils Qafzeh 6 and Skhul 5 have close similarities to those of Mladeč 5 and 6. It is possible that further studies on quantification of the features of the occipital morphology may help to resolve this issue.

In summary, this review shows that the relationship between Neanderthals and modern humans in Europe is far from being resolved. Although the Replacement model has gained in strength from the recent genetic, archaeological and palaeoanthropological data, morphological arguments can still support Assimilation and Multiregional evolution models. The scarcity of palaeoanthropological material from the key areas at the time of transition to Upper Palaeolithic and poor dating of some of the existing samples can also be listed among the obstacles to resolution of the argument. Smith *et al.* (2005) also note on the different conclusions resulting from different analytical approaches, such as cladistic versus multivariate statistical analyses.

The early archaeological and palaeoanthropological record from north-eastern Eurasia

The term 'north-eastern Eurasia' is used here to denote the territory formerly occupied by the USSR and now belonging to a number of independent states. This area encompasses a number of distinctive geographical areas that range from the Carpathians, Crimea, Caucasus, Tien Shan, Altai and Sayan mountain ranges and deserts of central Asia in the south to the current marshy lake-lands of the northern east European Plain, Ural mountains,

and tundra steppe to the north of the Polar Circle and vast, climatically variable and harsh Taiga and steppe areas of Siberia. Arguably, north-eastern Eurasia is a 'fringe' region for hominin distribution in the Pleistocene.

The earliest reliable evidence of hominin occupation comes from the Caucasus. The early Pleistocene site of Dmanisi yielded a number of fossils that date to over 1.8 million years BP whose taxonomic attribution is debated between *Homo habilis*, *Homo ergaster* or *Homo georgicus* (Gabunia et al., 2000; 2001; de Lumley et al., 2002; 2006; Lordkipanidze, 2003; Rightmire et al., 2006). In central Asia, pebble industry sites date to about 800,000 years BP (Kuldara) and 400,000–600,000 (Karatau and Lakhuti) in southern Tajikistan (Davis and Ranov, 1999). The Sel'Ungur site in Kyrgyzstan yielded hominin remains containing six teeth (three upper incisors and three lower premolars) belonging to two or three individuals and a fragment of a juvenile right scapula. These remains are associated with pebble industry underlying a layer that returned a uranium-thorium date of 126,000 \pm 5,000 years BP (Davis and Ranov, 1999).

Hoffecker (1999) summarizes information available from literature on the history of occupation of the European part of north-eastern Eurasia. He argues that prior to 250,000 years ago human settlements here were sparse and mostly confined to the southern regions. Both cave and open-plain sites are encountered, but there are no human remains associated with these sites. Archaeological artefacts reveal a flake industry without hand axes and only isolated examples of Levallois technology. According to Praslov (1995), the lack of settlements on the East European Plain prior to OIS stage 7 may be partly due to the effects of the extensive glaciations in the major river valleys as far as 50° north as well as marine transgression in the southernmost areas.

The Neanderthal sites of Eastern Europe range from the Last Interglacial (OIS 5e, 128,000 years BP) to the interstadial OIS 3 with most occupations dating to the Early Glacial OIS stages 5d to 5a (155,000 to 73,000 years BP) (Hoffeker, 1999). The Middle Palaeolithic sites are encountered not only in the southernmost mountainous regions of Crimea, Northern Caucasus and Carpathian mountains but also in the valleys of Dnestr, Pripyat, Dnepr, Desna, and Don rivers. Most of the localities contain Middle Palaeolithic artefacts. Cohen and Stepanchuk (1999) provide an overview of late Middle Palaeolithic and early Upper Palaeolithic evidence from the East European Plain and the Caucasus. They demonstrated that Middle Palaeolithic industries here belong to different traditions, such as Eastern Tabachian, Eastern Micoquian, para-Micoquian, Mousterian and Charentian. These industries continue until at least 40,000 years BP with few sites (such as Molodova in Dniester region and Il'skaya in Caucasus) providing for continuation of tradition into the Upper Palaeolithic. According to Cohen and Stepanchuk (1999), the most densely occupied areas in the late Middle Palaeolithic were Dniester region and Crimea. The youngest Middle Palaeolithic sites in Crimea are dated to about 30,000 BP in calibrated date (Zaskalnaya IV, Kabazi II) (Cohen and Stepanchuk, 1999). One site of the same age is also known from the Dnieper region (Zhornov, Layer II). The northern Caucasus seems to have been culturally isolated from the Great Caucasus and Transcaucasian region. Sites of para-Micoquian technology prevail in the northern Caucasus, whereas sites in the Great Caucasus and Transcaucasian region show similarities with more southerly Middle Palaeolithic, such as Typical Mousterian, Denticulate Mousterian and, probably, Charentian (Cohen and Stepanchuk, 1999).

The majority of human remains associated with Middle Palaeolithic industries are Neanderthals. Among them, postcranial remains of a child and an adult are known from Kiik-Koba (Bonch-Osmolovski, 1926; 1941; 1954) and cranial fragments from Zaskal'naya (Kolosov et al., 1975; Yakimov and Kharitonov, 1979) in the Crimea; a child mandible from Barakayevskaya Cave (Lyubin et al., 1986; Faerman et al., 1994), fragmentary remains from Monasheskaya cave (Belyaeva, 1992; Lyubin, 1994) and a complete skeleton of a very young infant and cranial remains of a 1- to 2-year-old Neanderthal child from Mezmaiskaya cave (Romanova and Kharitonov, 1995; Skinner et al., 2005) in the Northern Caucasus. In the Great Caucasus, Druzchula, layer II, and Bronsovaya Cave produced isolated teeth that appear to be *Homo neanderthalensis* in association with a typical Mousterian tool assemblage (Cohen and Stepanchuk, 1999). A fragment of an upper jaw of a Neanderthal was found at the Middle Palaeolithic layer 3d of Sakazhia, in the north-eastern part of the Black Sea area (Vekilova and Zubov, 1972; Vekilova, 1973; Nioradze et al., 1978). In the East European Plain, one tooth of inconclusive morphological affinity is known from Rozhok I at the Sea of Azov coast (Praslov, 1968), whereas a scapula from Shkurlat III at the Middle Don river (Shevyrev and Khrisanfova, 1984) and a femur from Romankovo at the Lower Dnepr river (Khrisanfova, 1965) were attributed to an archaic *Homo*. The Middle Palaeolithic layer at Starosel'e in Crimea yielded remains of a modern human child (Formosov, 1954; Formosov, 1958; Gerasimov, 1954; Roginski, 1954) but these have recently been claimed to come from an intrusive burial (Marks et al., 1997).

To the contrary of Cohen and Stepanchuk, (1999), Hoffecker (1999) points out that the lithic industry of the east European Neanderthals was fundamentally the same as that of their western European counterparts with the exception of rarer occurrence of Levallois

core technology, very small size of tools at some sites (Il'skaya I in the Northern Caucasus and Kiik-Koba in Crimea), and a high proportion and variety of bifacial tools. The Chokurcha site in Crimea yielded a unique form of triangles, absent anywhere in Western Europe. One location, Molodova I on the Dnestr River, possibly contains remains of an artificial shelter (Goretskii and Ivanova, 1982). However, Hoffecker (1999) notes that Neanderthal sites in Eastern Europe fail to yield evidence of recurrent use of bone, antler and ivory for the manufacture of finished tools even though these materials are present in many occupational horizons. Neanderthals seem to have abandoned the central East European Plain during the Last Glacial, when conditions possibly exceeded their capacity to cope with cold, dry climate (Hoffecker, 1999). The latest Neanderthal remains are known from the southernmost outpost of the area in question, the Mezmaiskaya cave in Northern Caucasus. The remains of an infant Neanderthal here returned a direct AMS date of 29,000 radiocarbon years BP (Ovchinnikov et al., 2000). However, this date is now believed to be the result of contamination by modern carbon and a later date was published by Skinner *et al.* (2005) who provide ESR ages for the Mousterian layers in Mezmaiskaya cave ranging from 36,000 to 73,000 \pm 5000 radiocarbon years BP. Matuzka cave in the same area was dated to 34,200 radiocarbon years BP \pm 1410 (Cohen and Stepanchuk, 1999).

To the east of the Caucasus, traces of Neanderthal occupations are known from Uzbekistan. The long-known find of cranial and postcranial remains of a 9-year-old Neanderthal child, found in association with Middle Palaeolithic industry at Teshik-Tash cave (Okladnikov, 1940; 1949) has recently been joined by human remains from Obi-Rakhmat Grotto (Glantz et al., 2004; Glantz et al., in press) and Anghilak cave (Glantz et al., 2003). The date for Teshik-Tash cave was mostly given on the basis of the lithic assemblage but Gromova

(1949) offered a correction to a Midle-Riss interstadial on the basis of the faunal remains from the site, which were similar to the present day warm interstadial conditions. At the moment, the Obi-Rakhmat occupational site is dated by U-series to 70,000–100,000 and ESR to 65,000–89,000 years BP. The material from Obi-Rakhmat (OR-1) is a juvenile represented by part of a permanent maxillary dentition and a fragmentary cranium. According to Glanz *et al.* (in press), these remains resist straightforward taxonomic identification with the dentition being relatively archaic but the cranium more ‘progressive’ in preserved features. The remains from Anghilak represent a taxonomically uninformative diminutive right fifth metatarsal (AH-1) and were derived from a layer that received an AMS date on charcoal of 27,000 years BP (Glanz *et al.*, in press). Both sites yielded Middle Palaeolithic technology, which allow Glanz *et al.* (in press) to bring up a question on the possibility that Middle Palaeolithic technology in this area was a product of anatomically modern humans. Other Middle Palaeolithic human remains from Central Asia include a discovery of a single deciduous lower lateral incisor associated with Middle Palaeolithic industry at Khudju, in Tajikistan (Trinkaus, 2000) and a few teeth and postcranial fragments from the Okladnikov cave, Northern Altai (Viola *et al.*, 2006). Technologically, Davis and Ranov (1999) attribute Middle Palaeolithic sites in Central Asia (Uzbekistan, Tajikistan, Kyrgyzstan) to Mousterian tradition. In addition to Teshik-Tash, Obi-Rakhmat and Anghilak, Davis and Ranov (1999) mention the Middle Palaeolithic sites of Kara Bura, Tajik, Khudzhi and Konoko in Tajikistan. The oldest site is Khonoko that was dated to about 200,000 years BP by association with a soil complex. The latest site is Khudzhi dated to 38,900 \pm 700 radiocarbon years BP (Davis and Ranov, 1999).

The earliest evidence of Upper Palaeolithic cultures in the European part of north-western Eurasia falls within the OIS 3 and 2. Dolukhanov *et al.* (2001) present a statistical review of radiocarbon dates for about 40 Upper Palaeolithic sites from this area and conclude that the occupational pattern can be divided into three stages. First, 41,000–36,000 years BP (in calibrated dates) corresponds to the OIS 3, or Middle Würm, a period of dry and cold climate in Western Europe and a prolonged, iceless ‘mega-interstadial’ period in north-western Russia. A few milder periods included ‘Grazhdanski Prospect’ attributed to 43,700–38,700 years BP (in calibrated dates) (Dolukhanov *et al.*, 2001). Sites of this period include earlier layers at Kostenki, Middle Don river, such as Kostenki 1/V, Kostenki 6, Kostenki 12/III, Kostenki 17/II (Bradley *et al.*, 1995; Dolukhanov *et al.*, 2001), and Kostenki 14/layers ‘hh’ and IVb (Sinitsyn, 2003; Anikovich *et al.*, 2006), Goncy in Southern Urals (Dolukhanov *et al.*, 2001) and Mamontovaya Kurya, located on the southern bank of the Usa river in the Arctic Circle, close to the polar Urals (Pavlov *et al.*, 2001). Therefore, at this time, human occupation encompasses almost all of the East European Plain. It is striking to know that human presence was recorded as far as the Polar Circle during OIS 3. However, there are also preliminary reports of even earlier Palaeolithic hominin presence in north-east Europe represented by undiagnostic archaeological artefacts from Elniki II at Kama River, northern Urals, which are dated to probably older than 125,000 years BP, and lower layers at Garchi I (same area), dated to earlier than 60,000 years BP (Pavlov *et al.*, 2004).

Unfortunately, there are very few hominin remains from the earliest occupational sites in European Russia. One human tooth is known from Kostenki 14 layer IVb (36,000 radiocarbon years BP) and two teeth come from Kostenki 17 layer II (36,000–37,000

radiocarbon years BP) (Sinitsyn, personal communication). The phylogenetic affinities of these teeth have still to be clarified. Thus, Hoffecker (1999) claims that one tooth from Kostenki 17 was classified as *Homo sapiens fossilis* (no reference is given). Sinitsyn (2003) reports on the assessment of the tooth from Kostenki 14 by Prof. A.A. Zubov (IAE RAS) as human and most possibly mongoloid.

The earliest layers at Kostenki 14 (layer IVb) and 17 (layer II) that were recently dated to over 40,000 years BP contain a unique Upper Palaeolithic technological complex not known anywhere else in Europe (Anikovich *et al.* 2006). However, other early occupational horizons at Kostenki also yielded cultural assemblages that were assigned to the 'Transitional' Streletskayan culture (Kostenki 11/V, Kostenki 12/II, Kostenki 14 layers IVa and 'hs') that is known for the combination of typical Upper Palaeolithic tool-kit (endscrapers, burins and splintered pieces), bone artefacts and art objects combined with Middle Palaeolithic bifacial points (Bradley *et al.*, 1995; Sinitsyn, 2003; Anikovich *et al.*, 2006). In the north-east of European Russia, similar tools were found at Mamontovaya Kurya (Pavlov *et al.*, 2001). Bradley *et al.* (1995) argue that typologically and chronologically, the Streletskayan derives directly from Middle Palaeolithic archaeological cultures in eastern European Russia. Middle Palaeolithic bifaces are abundantly found in the oldest Streletskayan layers of Kostenki (Kostenki 12/II and Kostenki 6) but in later layers, they gradually drop in proportion to Upper Palaeolithic tools. These bifaces also demonstrate development in technology with time by becoming thinner than any of the fully-bifaced artefacts from the Middle Palaeolithic assemblages in the former Soviet Union (Bradley *et al.*, 1995).

According to Dolukhanov *et al.* (2001), the next maximum concentration of radiocarbon-dated Upper Palaeolithic sites in the East European Plain is reached during the OIS 2, at 33,000–20,000 years BP, in calibrated dates. This period includes the Last Glacial Maximum and, according to the values of ^{18}O , corresponds to the coldest climatic conditions when the central region of the East European Plain was a periglacial zone (Dolukhanov, 2001). A number of assemblages from the multi-layered sites of Kostenki-Borschevo group in the Middle Don River correspond to this period (18 sites, according to Dolukhanov, 2001). Some of these sites contain Streletskayan cultural assemblages (see above). Other Upper Palaeolithic sites that show development from Streletskayan include later layers at Garchi I, dated to 29,000 radiocarbon years BP (Bradley *et al.*, 1995; Pavlov *et al.*, 2004), Biryachaya Balka, in the lower reaches of the Severski Donets, and a rich site of Sungir', near the town of Vladimir in the Klyasma River Basin (Bradley *et al.*, 1995) that is presently on average dated to 29,000 \pm 922 in calibrated years BP (Dolukhanov *et al.*, 2001; but see Kuzmin *et al.*, 2004). Location of such sites as Sungir', Garchi I, Byzovaya and Zaozer'e mark the occupational border of the periglacial zone during the Last Glacial Maximum (Pavlov *et al.*, 2001; Pavlov *et al.*, 2004).

Typically, Upper Palaeolithic industries are recorded from a great number of sites on the East European Plain, which are collectively labelled as 'Eastern Gravettian' (Dolukhanov, 2001). Their distribution is especially dense to the south of 55° North around the area of the Black Sea and its tributaries. Grigor'ev (1993) and Soffer (Soffer, 1993) suggest that the peopling of eastern Europe happened via a gradual overflow of populations from central Europe in an easterly direction as confirmed by older dates for the majority of sites in central Europe at that time. Cohen and Stepanchuk (1999) present a detailed description of

variability, interaction and transition between Middle and early Upper Palaeolithics in the East European Plain and Caucasus. These authors argue that early Upper Palaeolithic evidence here demonstrates a complicated picture of coexistence of sometimes sharply different industries, for example, the analogous transition in Europe to the Aurignacian and Gravettian and original 'Transitional' industries, such as Streletskayan.

From this period, human remains are now known from a number of localities in Kostenki, such as male cranium Kostenki 2, male cranial and postcranial remains from Kostenki 14, cranial and postcranial fragments of a child's from Kostenki 15 (in matrix), and child cranium and mandible from Kostenki 18 (Praslov and Rogachev, 1982). The site of Sungir' yielded cranial and postcranial remains of up to 9 individuals. The most prominent are two richly adorned burials, one of a 50- to 55-year- old male and the other of two children, most possibly a boy and a girl, of 11 and 9 years of age, respectively (Alexeeva et al., 2000).

The latest Upper Palaeolithic peak of occupational sites comes in the period 18,000–15,000 years BP which completely disappear from the East European Plain by 11-12 calibrated years BP (Dolukhanov et al., 2001; 2002) This peak coincides with the recession of the ice sheets and a rapid increase in temperature and the summer insulation (Bradley, 1995).

During this period, sites concentrate along major waterways, especially Dnieper and its tributaries, Desna and Sudost', the Diester basin, Don and the littoral of the Sea of Asov (Dolukhanov, 2001). No human remains have been explicitly attributed to this period so far.

In addition to the fossils discussed above, there are poorly dated frontal bones from Skhodnya (Gremyatski, 1952b) and Khvalynsk (Bader, 1940; 1952b; Gremyatski, 1952a)

in the East European Plain and one frontal bone from Podkumok in the northern Caucasus (Gremyatski, 1922; 1948; 1934) that have been claimed to belong to Upper Palaeolithic times. A fragmentary cranium has been recovered from Satanay grotto in northern Caucasus, which received preliminary dating to OIS 2 (Romanova and Kharitonov, 1984). In central Asia, two adult fragmentary mandibles were recovered in association with Upper Palaeolithic industry at Samarkandskaya in Uzbekistan (Ginzburg and Gokhman, 1974).

The Siberian Middle and Upper Palaeolithic record within the limits of resolution of radiocarbon methods has been recently summarized by Dolukhanov *et al.* (2002). In contrast with Dolukhanov *et al.* (2001), Dolukhanov *et al.* (2002) provides for uncalibrated radiocarbon dates for each site referring to the fact that calibration does not affect the general trend in the data. These authors quote the earliest occupation from Altai Mountains (caves of Cara-Bom, Kara-Tenesh, Okladnikov, Strashnaya, Denisova and Anui 2 and an open-air site Ust-Karakol) falling within the range of 43,000–30,000 radiocarbon years BP. Cultural assemblages at all these sites have Mousterian character, apart from Kara-Bom, which also includes up to six strata with a higher proportion of Upper Palaeolithic blade tools (Derevyanko *et al.*, 2000). The Okladnikov cave yielded five human teeth and three postcranial fragments that were not found to be different from modern humans (Alexeev, 2006). A number of sites of the same age span are known from Enisei and Angara River Valleys (Kamennyi Log, Kuttak 4, Ust-Kova, Military Hospital and Druzhiniha). To the south, sites dated to 33,000–39,000 radiocarbon years BP were found at River Lena (Makarovo 3), in Buryatia (Kamenka-1) and in Trans-Baikal area (Artin 2 at Khilka and Artin Rivers) (Dolukhanov 2002).

According to Dolukhanov (2002), the middle stage of Siberian occupation is dated at 25,000–17,000 years BP and is marked by numerous sites from Yenisei and Angara Rivers (see also Derevianko and Markin, 1998). Human remains are known from the ‘twin’ sites at Angara, namely Mal’ta and Buret, representative of two or three modern human children (Alexeev and Gokhman, 1987; Sitlivy et al., 1997).

The last period of the Upper Palaeolithic in Siberia falls within 17,000–10,000 radiocarbon years BP and includes a great number of sites from Minusinsk depression on the middle stretches of the Yenisey River and the Sayan foothills as well as a group of sites in the Trans-Baikal region of southern Siberia (Dolukhanov, 2002). Human remains are known from the site of Afontova Gora 2 in Minusinsk depression. This collection includes a fragment of the frontal, a radius, humerus and a child’s dentition belonging to a modern human (Alexeev and Gokhman, 1987).

Further to the east, the earliest sites are known from Aldan River in Yakutia (Ust-Mil and Ihnie-2) dated to 33,000–31,000 radiocarbon years BP and containing an indigenous culture, different from contemporaries in western Siberia or Europe (Dolukhanov, 2002). In the Maritime area, one site (Geograph Society Cave) was reported to date to 36,000 radiocarbon years BP (Derevianko, 1998; Dolukhanov et al., 2002). Later sites from Aldan and Zeya Rivers are dated at about 20,000 years BP as well as one site from Sakhalin Island which received a similar date (same references). The majority of Upper Palaeolithic sites are confined to the later stage of occupation and concentrate around the Aldan River (three sites) as well as the Arctic coast (one site) and the Kolyma River basin (one site) (Dolukhanov, 2002). The most eastern occupations are marked by the stratified site of Ushki 1 in Kamchatka Peninsula (dated around 14,000–10,000 radiocarbon years BP), and

two sites from the Maritime Region (Ustinovka 6 and Suvorovo 4, dated at about 14,000 and 15,000 radiocarbon years BP). Two sites located along the lower stretches of the Amur River, which were dated at about 13,000 radiocarbon years BP already contain fragments of ceramic ware (Derevianko and Medvedev, 1995; Kuzmin and Orlova, 2000; Dolukhanov *et al.*, 2002) .

In summary, according to Dolukhanov *et al.* (2002), the earliest late Pleistocene occupation of Siberia may be traced to 43,000–30,000 radiocarbon years BP. The peaks of Upper Palaeolithic site density in Siberia fall at 16,000–12,000 radiocarbon years BP for south-central and 14,000–10,000 radiocarbon years BP for north-eastern regions. Kuzmin and Keates (2004) criticise Dolukhanov *et al.* (2002) for using a biased sample of sites in the analysis. These authors provide a list of older dates for some sites used by Dolukhanov *et al.* (2002) or sites with older radiocarbon dates that were not included in the above work at all thus affecting the final conclusions. Kuzmin and Keates (2004) argue that the occupational density of southern Siberia was already quite high since ca. 43,000 and increased between 31,000 and 19,000 radiocarbon years BP. The later stages have maximum site density despite deterioration of the climate during this time. Kuzmin and Keates, (2004) argue that given the scarcity of sites of that age in eastern Europe, the colonization of northern Eurasia could have happened in an east-to-west direction, rather than the west-to-east direction implied by Dolukhanov *et al.* (2002).

In total, it appears that the earliest settlements of North-Eastern Eurasia are confined to the southern mountainous regions of the Caucasus, Uzbekistan and Altai. Dates of 46,000–32,000 radiocarbon years BP are known for the Altai region with sites of this age containing Mousterian–Upper Palaeolithic transitional assemblages (Derevyanko, Petrin

and Rybin, 2000). Although Mousterian sites from Crimea, Caucasus and Uzbekistan provide an association with Neanderthal human remains, there is no such association evident for Altai. The sites of 40,000–32,000 radiocarbon years BP are already widely spread across the East European Plain, form a dense concentration in Altai, and are found on Yenisey River, Lake Baikal, Trans-Baikal Region, Yakutia and the Far East. Many of these sites contain either Middle Palaeolithic or ‘Transitional’ Middle-to-Upper Palaeolithic assemblages but, for the rare exception of the Teshik-Tash site, there is no direct evidence that any of them are left by Neanderthals. A few fossil remains from Rozhok 1, Okladnikov Cave, and now Obi-Rakhmat and Anghilak, do not allow for their interpretation as Neanderthal. This fact prompts Dolukhanov *et al.* (2002) to draw parallels between Middle Palaeolithic sites in North-Eastern Eurasia and the situation in Levant, where anatomically modern humans coexisted with Neanderthals and most possibly produced the same type of ‘Levantine Mousterian’ technology. In addition, there is obvious similarity with the contemporary sites of ‘Transitional’ Bachokirian tradition in Bulgaria (whose calibrated date is over 43,000 years BP or 38,000–37,000 radiocarbon years BP) that yielded undeterminable human remains and a finding of *Homo sapiens* remains at the Late Palaeolithic site of Salawusu in Inner Mongolia that yielded technology with abundant archaic (Middle Palaeolithic) elements. Dolukhanov *et al.* (2002) argue that the Palaeolithic sites in northern Eurasia radiocarbon dated to 46,000–32,000 years BP reflect the initial colonization of this area by anatomically modern humans regardless of the character of the lithic industry. These authors maintain that the colonization of northern Eurasia must have started from the core area in Levant, where anatomically modern humans were already present at 100,000–80,000 years BP.

Frontal bone: Comparative morphology and evolution

Frontal bone morphology is especially controversial in the Late Pleistocene hominins, including Neanderthals and early modern humans. Recent studies that address frontal bone morphology in modern humans and early *Homo*, including Neanderthals, can essentially be divided into three groups. The first group of studies incorporates the frontal bone as part of the whole cranium and frequently addresses the questions of homology and apomorphies in evolution with the help of comparative ontogenetic studies (Lieberman, 1995; 1998; 1999; Tiller, 1989; 1998; Lieberman and McCarthy, 1999; Lieberman et al., 2000a; 2000b; 2001; McCarthy and Lieberman, 2001; Ponce De León and Zollikofer, 2001; Lieberman et al., 2002; Minugh-Purvis and McNamara, 2002). The second group of studies uses morphological aspects of the frontal bone in adult individuals for discrimination between groups of the fossil *Homo* and recent modern humans and inferences on the origin of the geographical and temporal variation patterns. This literature is extremely vast so that it makes sense to review a few recent studies, which represent the current state of the knowledge in the field. The last set of literature related to the frontal bone morphology discusses functional and spatial aspects of the evolution of the circumorbital morphology in primates. Here I concentrate on the studies that are relevant to the higher primates and hominins.

The frontal bone as part of the cranium

Recent studies by Lieberman *et al.* (2002) have important implications for comparative cranial morphology. They argue that anatomically modern humans are identified by two general structural autapomorphies: facial retraction and neurocranial globularity.

Lieberman *et al.* (2002) reach their conclusion on the basis of factor analysis of external cranial characters of 100 recent modern human skulls from craniofacially diverse populations around the world (both sexes in equal proportion), 10 Late Pleistocene fossils commonly identified as anatomically modern *Homo sapiens* and nine crania of archaic *Homo*. The same authors investigate into reasons that underlie the specific differences in craniofacial morphology by comparing ontogenetic series of mid-sagittal radiographic projections of modern humans and chimps. They conclude that major variables that apparently underlie differences in facial retraction and neurocranial globularity between archaic *Homo* and anatomically modern humans are the same as those that contribute to similar differences in cranial ontogeny of human and chimpanzee: cranial base angle, the relative length and width of the cranial fossae and relative facial height and length.

Spatial relationships between the cranial base and the face in relation to supraorbital morphology have been investigated by Lieberman (1998; 2000) in modern humans, extinct hominins and chimpanzees. In 1998, Lieberman suggested that a number of characteristic modern human facial features, such as a vertical forehead, a diminutive browridge, lack of facial projections, 'stem partly from a single, ontogenetically early reduction in the length of the sphenoid' (Lieberman, 1998, p. 158). This conclusion implied that Neanderthals and other archaic *Homo* should be excluded from *H.sapiens* on the basis of the suggestion that archaic forms did not have as short a sphenoid as modern humans. However, Spoor *et al.*

(1999) subsequently refuted Lieberman's conclusion in the part relating to Holocene and Late Pleistocene anatomically modern *H.sapiens*. These authors made new measurements of the anterior sphenoid length and midfacial projection and found that the anterior sphenoid length was initially incorrectly estimated in the archaic fossil crania. It turned out that the anterior sphenoid in modern humans is no shorter than in archaic *Homo*.

An interesting adjustment to these results was made by O'Higgins (2000). Having performed morphometric analysis of the shape of face and basicranium on lateral radiographs of modern humans and archaic hominins, he found that there is a shift in form of the anterior cranial fossa in modern humans which looks like it is shortened compared to that of fossil hominins. O'Higgins suggests that the relative compression of the area of the anterior sphenoid actually indicates a localized region that is particularly stable in comparison with the whole landmark configuration. According to O'Higgins (2000), in modern humans, the upper face is repositioned and reduced relative to the upper cranial base.

The later work by Lieberman *et al.* (2004), which was largely made on the basis of the same material as used by Lieberman *et al.* (2002), argues that the evolutionary change occurs by small-scale shifts in development that could be observed in the fossil record. These authors conclude that facial retraction in modern humans is largely a product of three derived changes: a relatively longer anterior cranial base, a more flexed cranial base angle and a relatively shorter upper face. Epigenetic integration of these parts of the cranium produces the effect of the facial retraction in modern humans.

Bookstein *et al.* (2003) also address the question of integration in the skull by comparing cross-sectional ontogenetic data from modern humans and adult Pleistocene hominins. They employed methods of geometric morphometrics, which permitted identification of how the cranial base, face and neurocranium are integrated in *Homo*. Singular warp analysis of the midsagittal plane has revealed that vault, cranial base and face show localized patterns of covariation with ontogeny, similar, but not identical in the patterns seen with evolution. The principal differences between ontogeny and phylogeny pertain to the cranial base. This work calls for caution when interpreting ontogenetically homologous processes in the cranial base in terms of their phylogenetic implications.

A substantial part of the recent literature pays special attention to the ontogeny of Neanderthals in comparison with the modern humans in the attempt of identification of homologies and autapomorphic features in these species. In Ponce de Leon and Zollikofer (2001), an ontogenetic approach is applied to the study of the extent of cranial morphological differences between Neanderthals and early modern humans. These authors show that Neanderthal cranial autapomorphic features appear in early ontogeny and persist throughout life implying almost parallel ontogenetic trajectories in the two species. Ponce de Leon and Zollikofer (2001) use geometric morphometric analysis of CT scan three-dimensional images. Whole crania of young and adult Neanderthals, early modern humans and recent modern humans, available to these authors, were analysed.

Ponce de Leon and Zollikofer's conclusion corresponds to earlier studies of dentition of young Neanderthals (Legoux, 1970; Wolpoff, 1979; Heim, 1982; Dean *et al.*, 1986; Stringer *et al.*, 1990) and Neanderthal robusticity (Heim, 1982; Trinkaus, 1986). In general, Neanderthals appear to show accelerated development of the neurocranium compared to

dental age and develop features of robusticity. Tattersall and Schwartz (2000) stress that some Neanderthal autapomorphic morphologies (such as medial projections within the Neanderthal nasal cavity, the large nasal region and protruding snout) are already present in children as seen in the 3-year-olds from Pech de l'Azé, Roc de Marsal and Subalyuk and a 9-year-old from Teshik-Tash. The Teshik-Tash 9-year-old juvenile already had distinctive swellings in the supraorbital region. A 15-year-old teenage Neanderthal from Le Moustier already had a better-formed browridge (Tattersall and Schwartz, 2000; Ahern and Smith, 2004).

Children of the early anatomically modern humans from Skhul and Qafzeh in Levant, according to Tiller (1989), do not share any of the Neanderthal autapomorphies, such as 'en-bombe' cranial shape and nasal protrusion. They display a mosaic of primitive and modern cranial features (Tab.2.1) some of which are shared with the recent modern humans and some with Neanderthals and other archaic hominins. This result enables Tiller (1989) to argue that recent modern humans have closer relationships with the Skhul and Qafzeh hominins than with the Neanderthals.

Table 2.1 Mosaic of features in Skhul and Qafzeh immature individuals. Summarised from Tiller (1989).

<i>Type of features</i>	<i>Description</i>
1. Juvenile features which are common to all children within <i>Homo sapiens</i> (including Neanderthals)	Bone ossification framework; accentuated sagittal frontal curvature with marked frontal eminences, slight external occipital structures.
2. Primitive retentions shared with archaic <i>Homo sapiens</i> (or at least Neanderthals)	Large biasterrionic breadth; molar pattern; relatively robust bone framework of mandible compared to modern children. Among mandibular elements: torus transversus, a slight planum alveolare on Qafzeh 4 and a fossa genioglossa on Qafzeh 4, 10, 15. Large teeth are known for Qafzeh 5, 10 and 15.
3. Primitive retentions	Mandibular elements: tuber symphyses, fossae mentales and a rough

shared with both Neanderthals and modern children	shape of incurvatio mandibulae; Qafzeh II has large inter-orbital breadth and porion-bregma height; frontal arc is longer than the parietal one; tympanic plate is divided into two unequal parts (anterior and posterior) by a slight crest separated from the mastoid process; robusticity indices of the mandibular body between the first and the second molars; flexed maxilla with a canine pit; weak juxtamastoid eminence; lateral (transverse) shortness of tympanic plate; the slenderness of the mandible with a salient chin and small teeth (with the exception of canines and premolars).
4. Modern autapomorphies displayed by immature and adult Proto-Cromagnoids	Chin eminence; neurocranial globularity; glabellar eminence and the supraorbital morphology are more developed than in modern European children but clearly distinct from those of Neanderthals.
5. Modern features present in immature Proto-Cromagnoids and immature modern crania	Accentuated sagittal frontal curvature; marked frontal eminences; slight external occipital structures.

The majority of researchers agree on the differences in morphological development between Neanderthals and modern humans. However, some studies are not in line with the general view on Neanderthal comparative growth and development. For example, Odwak (2000; 2001) analyses postcranial remains of Amud child from west Asia and comes to the conclusion that robusticity of this 10-month-old child does not fall outside the range of modern human variation. Strand-Vidarsdottir (1999) found that many Neanderthal autapomorphies do not develop until later in ontogeny, as opposed to the conclusion by Ponce de Leon and Zollikofer (2001). Moreover, Strand-Vidarsdottir (1999) argues that the morphological pattern of differences between Neanderthal and modern infants is not the same as between adult Neanderthals and adult modern humans. Neanderthal children have more orthognatic midface, relatively posteriorly located and higher orbits, a wider frontal, relatively wider anterior alveolae and a relatively more posterior orientation of zygomatic bones and lateral parts of the maxillae. Neanderthals have a unique growth vector where orbit size undergoes relative reduction by means of a dramatic contraction of the upper half of the orbit. Supraorbital torus becomes almost horizontal as a consequence. There is also a marked vertical contraction of the entire supraorbital area. Midface and nasal aperture increase dramatically. Unlike in modern humans, there is no lateral expansion of the zygomatic bones in Neanderthals.

In sum, it appears that autapomorphic modern human features of the facial retraction and neurocranial globularity on one hand, and the autapomorphic Neanderthal features, such as 'en-bombe' shape of the neurocranium, nasal protrusion and others appear early in ontogeny confirming specific level of differences between the two hominin groups. The early Anatomically Modern Humans from Levant lack the Neanderthal autapomorphies but

still preserve a number of primitive features in their cranial morphology that they share with both, the archaic *Homo* and Neanderthals. The presence of the modern human autapomorphies in the Skhul and Qafzeh hominins from the infancy implies their closer relationship with the recent modern humans.

Frontal bone morphology in the comparative studies of fossil *Homo*

A number of studies focus on the temporal and geographical variation in hominin frontal bone morphology. The work by Bookstein *et al.* (1999b) is an example of a study that is relevant for the frontal bone morphology of the complete genus *Homo*. These authors investigate the temporal pattern of variation in the frontal bone by comparing external and internal midsagittal outlines of the frontal in modern humans and archaic hominins.

Material included sagittal CT scan profiles of five mid-Pleistocene and Neanderthal crania and 16 modern humans. The profiles of the frontal bone were compared with the help of geometric morphometrics. After scaling to the centroid size by means of Procrustes superimposition, it was found that differences between archaic and modern individuals were confined to the external outline of the frontal bone, especially the region around the browridge. However, the shape of the inner median-sagittal profile appeared to be remarkably stable over all 21 specimens: ‘...the inner profiles of the frontal bone are statistically indistinguishable implies that mid-sagittal vault morphology may likewise have retained remarkable conservative in the genus *Homo* since the mid-Pleistocene’ (Bookstein *et al.* 1999, p.220). Statistical analysis demonstrated that the change in hominin brain size

from pre-Pleistocene to the present was not coupled with the change in the shape of the inner frontal bone.

The value of the external features of the frontal for the assessment of variation between hominins has been acknowledged by Athrea (2006) who made an attempt to find geographical pattern in such variation among Middle and Late Pleistocene hominins. She analyses 46 fossils from Africa, Asia and Europe with the help of Fourier analysis of the several outlines across the frontal bone. This author tested the hypothesis that the morphological variation mirrors the genetic evidence for isolation-by-distance and presents her results for each of the chosen five frontal outlines (transverse across maximum and minimum breadths, sagittal and para-sagittal outlines at 50% and 25% of the hemi-cranium) separately. However, she found that only the sagittal outline corroborates the working hypothesis, whereas all other outlines either provide no support or provide the evidence to the contrary (i.e. distant fossils can be more similar than neighbouring ones). Given that Athrea (2006) accounted for the time differences between fossils in her work, the revealed pattern brings this author to the conclusion that the differentiation among Late Pleistocene fossils does not mirror the genetic evidence for isolation-by-distance in shaping frontal bone variation among regional populations of mid-Pleistocene *Homo*.

To the contrary of the results of Athrea (2006) on the frontal bone of the Middle and Late Pleistocene fossils, Lahr (1996) and Lahr and Wright (1996) demonstrate presence of geographical and temporal pattern in distribution of the features of robusticity in modern human populations. These features include development of cranial suprastructures listing size and shape of the supraorbital relief among them. The above authors first of all argue that the 'robusticity' complex is highly positively correlated with two particular aspects of

the cranial morphology, e.g. the general size of the cranium and its long antero-posterior and narrow transverse diameters. As a result, fossil crania of the early and epi-palaeolithic modern human tend to be larger and thus display larger development of the cranial suprastructures. The same is applicable to a number of isolated recent human populations, such as Fuegian-Patagonians and Australo-Melanesians. The Australians, however, differ by relatively smaller crania that are long and narrow but have large palates, a set of features that also demonstrated large correlation with the development of the cranial suprastructures. Sub-Saharan Africans, South East and East Asian populations tend to have smaller and wider crania and hence smaller development of the suprastructures, whereas European populations take intermediate position between the extremes.

The shape of the supraorbital relief in particular has been claimed to display specific features in recent modern humans and in the Neanderthals (Cunningham, 1908; Smith and Ranyard, 1980). In other groups of hominins, descriptions of the supraorbital morphology do not generalise up to a specific level, for the rare exception of the Asian *Homo erectus* (Weidenreich, 1939; 1943b; Weidenreich, 1951). Smith and Raynard (1980) offer a detailed definition of the morphology of the Neanderthal browridge. The latter represents an osseous bar projecting from the frontal squama at the inferior border of the frontal bone and arching from glabella laterally over each orbit to the frontozygomatic suture. There is a depression in the torus above the glabella. The Neanderthal supraorbital torus continues laterally into the so-called lateral orbital pillars. Adult Neanderthals have expansive frontal sinuses that occupy most of the glabellar segment of the torus and extend well into the orbital segment. Unlike in Neanderthals, the supraorbital region in modern humans, including those from the Late Pleistocene, does not form a continuous browridge. Instead, it

is divided into the superciliary arch or ridge and the supraorbital arch (Cunningham, 1908, cited by Smith and Raynard, 1980). The superciliary arch extends from glabella over the medial third to half of the orbit. The supraorbital arch is located over the lateral portion of the orbital margin. The supraorbital arch has been further subdivided into the supraorbital margin and trigonum or planum supraorbitale. The supraorbital margin usually begins at the supraorbital notch or foramen and extends to the frontozygomatic suture. It can also extend under the lateral portion of the superciliary ridge, being separated from the latter by a variably pronounced groove (the supraorbital sulcus). Trigonum supraorbitale represents the upper plane of the supraorbital margin. This plane is not structurally separable from the latter.

It has been claimed that there is a continuity in the change of the features over the period of Neanderthal decline and the appearance of the modern humans (Smith and Ranyard, 1980; Smith et al., 1989b) at least in eastern Europe. Smith and Raynard (1980) concentrated their study on the browridge morphology in Upper Pleistocene fossil hominins from south-central Europe and included subadult individuals as well as adults. Their Neanderthal sample included fossils from Šal'a, Subalyuk, Krapina and Vindija among others. The Upper Pleistocene modern humans included fossils either associated with Aurignacian (30,000–35,000 radiocarbon years BP) or Gravettian (25,000–30,000 radiocarbon years BP) Upper Palaeolithic cultures. They document a trend towards gracilisation of the east European Neanderthals (expecially well seen in the Vindija sample) and continuity of the trend of the supraorbital relief reduction into the Upper Palaeolithic modern humans in eastern Europe. In contrast, the pattern of change in the supraorbital region in western Europe points to an abrupt transition from Neanderthaloid form to that in modern human,

thus suggesting rapid replacement of populations (Smith et al., 1989b). One of the interesting features shown by this study is that medial thickness of the supraorbital region demonstrates no significant pattern of change over time. The authors feel that this lack of change is an artefact of the invasion of the lower frontal squamae by the frontal sinus in early modern humans, a condition not found in Neanderthals (Smith et al., 1989b).

A single-region approach is used by Sladek *et al.* (2002) in multivariate analysis of the morphological affinities of Šal'a frontal bone. These authors use inter-landmark distances together with a number of discrete traits of supraorbital morphology to compare Šal'a with Middle and Late Palaeolithic hominins, including Neanderthals, early and recent modern humans and found that a) Neanderthals are clearly separated from modern humans by multivariate analysis but not from other Middle Palaeolithic fossils and b) by combination of features of the supraorbital relief and general proportions of the frontal Šal'a fits into the category of a Late Pleistocene representative of the central European Neanderthal sample. Sladek *et al.* (2002) also demonstrate a trend of reduction of the supraorbital relief in time from Middle- to Late Pleistocene fossils and modern humans where Neanderthals take an intermediate position. This paper represents an example of successful morphological analysis of the total shape of the cranial fragment and its conclusion differs from the interpretation of a 'Transitional' character of Šal'a morphology previously reported on the basis of anatomical detail (Jelínek, 1969; Smith and Ranyard, 1980; Smith, 1992; 1984; Wolpoff, 1999).

Smith and Raynard (1980) also give a description of the browridge form in young Neanderthal individuals. Thus, in specimens younger than 6 or 7 years of age, the torus is only visible as a slight bulging from the squama, faintly outlined across the supraorbital

region. Nevertheless, it extends as a continuous structure across the orbits and interorbital area by about 5 years of age. Younger specimens seem to have some division between toral segments. Older subadults, like Le Moustier (estimated 15 years of age) and Krapina cranium E, exhibit tori very close in overall form and size to those of adults, but lack the final aspects of the growth and remodelling process to produce the characteristic Neanderthal torus. This results in significant difficulties in the interpretation of some samples and may cause incorrect specific assignment. Smith and Raynard suggest placing individuals into three general age categories on the basis of the combination of the degree of development of the frontal sinus, constitution of the anterior sinus wall, amount of bone deposition characterized by the presence of the vermiculate pattern, build-up of bone laterally between the frontozygomatic suture and frontotemporale, and the general degree of torus projection and separation from the squama. In development of this idea, Ahern and Smith (2004) suggest usage of the Le Moustier 1 adolescent Neanderthal as a type specimen for comparison and identification of immature fossil remains.

The listed above studies demonstrate an important place of the frontal bone external morphology for the differentiation of hominin groups. The pattern during the transition from the Middle to Late Pleistocene and Holocene reveals a trend towards reduction of the frontal bone superstructures some part of which, at least in modern humans, is related to the decrease in size of the crania. In Middle and Late Pleistocene hominins, however, no geographical pattern has been revealed to date. To the contrary, modern humans display a clear geographical pattern of variation. The trend of the reduction of the supraorbital relief takes a slightly different direction in modern humans due to subdivision of their supraorbital relief into separate portions. This contrasts with the morphology in archaic

hominins, where supraorbital relief forms a continuous torus. Some modern human populations may display more developed robusticity complex as correlated either with the generally larger size of their crania or particularly long and narrow shape of the neurocranium.

Circumorbital morphology in primates

The third group of papers is specifically focused on circumorbital morphology. This subject is, on one hand, investigated from the point of view of the functional basis for the browridge development in primates in general and, on the other hand, in application to the phylogenetic differences between Late Pleistocene hominins. The research on the functional evolution of the browridge is represented by two competing hypotheses. The first states that the evolutionary development of the browridge is related to masticatory stresses. In other words, the browridge develops as a reinforcement of the upper face in response to anterior or lateral masticatory stresses (Endo, 1966; Oyen et al., 1979a; 1979b; Wolpoff, 1980; Oyen and Russel, 1982; Russel, 1985; Greaves, 1985; Rosenberg, 1986). The second hypothesis argues that browridges develop as a byproduct of the neuro-orbital disjunction, i.e. they 'fill in' the space between the face and neurocranium in some primates who have their faces positioned anteriorly to the neurocranium. The best account of the details of this discussion is given by Ravosa (1988; 1991a; 1991b).

Bookstein *et al.* (1999b) support the masticatory stress hypothesis by interpreting the large frontal sinuses in Pleistocene hominins as a sign of adaptation to high masticatory stresses. Large anteriorly projecting browridges are frequently hollowed in Pleistocene hominins. They have relatively thin outer walls and a range of internal lamellae support, which

minimizes the bone mass without compromising the necessary strength. Numerous small walls may help to absorb the masticatory stress. Ravosa *et al.* (2000) have challenged this conclusion on the grounds that there is both experimental and morphological evidence that directly supports the spatial model of supraorbital torus formation to the detriment of the masticatory stress hypothesis. *In vivo* experiments on baboons, macaques and owl monkeys show that strain magnitudes generated by chewing forces throughout the supraorbital region are uniformly low even during the mastication of hard objects (Hylander et al., 1991; Hylander and Ravosa, 1992; Ross and Hylander, 1996). Such strains are most probably insufficient to induce bone deposition (Frost, 1986; Frost, 1988; Martin and Burr, 1989).

In addition, Ravosa (1988, 1991a) and Hylander and Ravosa (1992) illustrate the lack of any correlation among anthropoids between the dimensions of the browridge and the moment of arms of the major masticatory muscles. Ravosa's (1988, 1991a, 1991b) analyses of an interspecific sample of 92 primate species and intraspecific ontogenetic sample of *Macaca fascicularis* show that face size is the primary determinant of variation in primate circumorbital morphology. According to his work, anteroposterior browridge thickness is correlated with neuro-orbital disjunction among anthropoid primates, i.e. distance between neurocranium and face.

Lieberman (2000) elaborates on the hypothesis of the influence of the spatial relationships between the face, basicranium and neurocranium on the development of the supraorbital relief in humans, fossil *Homo* and chimpanzees. He demonstrates that browridge length is tightly correlated with the midfacial projection in these groups and the midfacial projection, in its turn, results from the relationships between the length of the anterior cranial base, sphenoid length and the length of the midface. Basing on the longitudinal radiographic

study of modern humans (Denver Growth study) and a cross-sectional study of chimpanzees he concludes that humans and chimps have a different pattern of relationships between these lengths implying non-homologous origin of the supraorbital relief in two species. It appears that archaic *Homo* also differs from modern humans in this parameter, thus suggesting that supraorbital relief in modern humans is not homologous to the browridges archaic hominins. In addition to the influence of the spatial relationships, Lieberman (2000) demonstrates that allometry, i.e. a phenomenon where forms of different sizes are not isometric (Jungers et al., 1995a), also tends to affect the size of hominin browridge.

At present, many authors agree that the evolution of the browridges in primates is better attributed to the effect of the neuro-orbital disjunction due to the anterior position of the face in primates by the majority of authors. Modern humans, to the contrary with other primates in general as well as with the archaic *Homo* in particular, have different pattern of integration in the face that might suggest the non-homologous origin of their supraorbital relief.

Morphology and ontogeny of the frontal bone in modern humans

General

The frontal bone forms the larger portion of the upper face. The vertical part of the frontal bone, its squama, represents a part of the roof and sidewalls of the cranial cavity, whereas its horizontal portion forms the floor of the anterior cranial fossa and the roofs of the orbits. In total, the human frontal has a bowl-shape and articulates with the parietals, greater wings

of sphenoid, zygomatics, frontal processes of maxillae, lacrimals, nasals and the cribriform plate of the ethmoid.

Ectocranial surface

In modern humans, the external surface of the frontal bone is rather smooth (Fig. 2.1). The area of the greatest curvature of the bone, forming the rounded tuber (eminentia) frontale, lies above the centre of each orbital margin (Scheuer and Black, 2000). A prominence at the centre of the external surface of the squama above the nose is conventionally known as the glabella. Laterally on each side of the glabella, two elevations form superciliary arches above the orbits. A supraorbital foramen or supraorbital notch pierces each supraorbital margin of the frontal bone.

The squama of the frontal bone articulates posteriorly with two parietal bones via the highly serrated coronal suture. Bregma is at the site of the junction of the three bones and is the site of the former anterior fontanelle (Scheuer and Black, 2000). The lateral part of the orbital margin leads to the zygomatic process, which articulates with the zygomatic bone. Between the lateral end of the coronal suture and the zygomatic process is a thickened, triangular area for articulation with the greater wings of the sphenoid. In anatomical jargon, this region of articulation is called the pterion.

The inferior-most point on the external surface of the frontal bone in the midline is the nasion, a point of frontal bone articulation with two nasal bones.

Anterior attachments of the temporal muscles are delimited as superior and inferior temporal lines, which extend posteriorly over the frontal portion of the bone (Aiello and Dean, 1990).

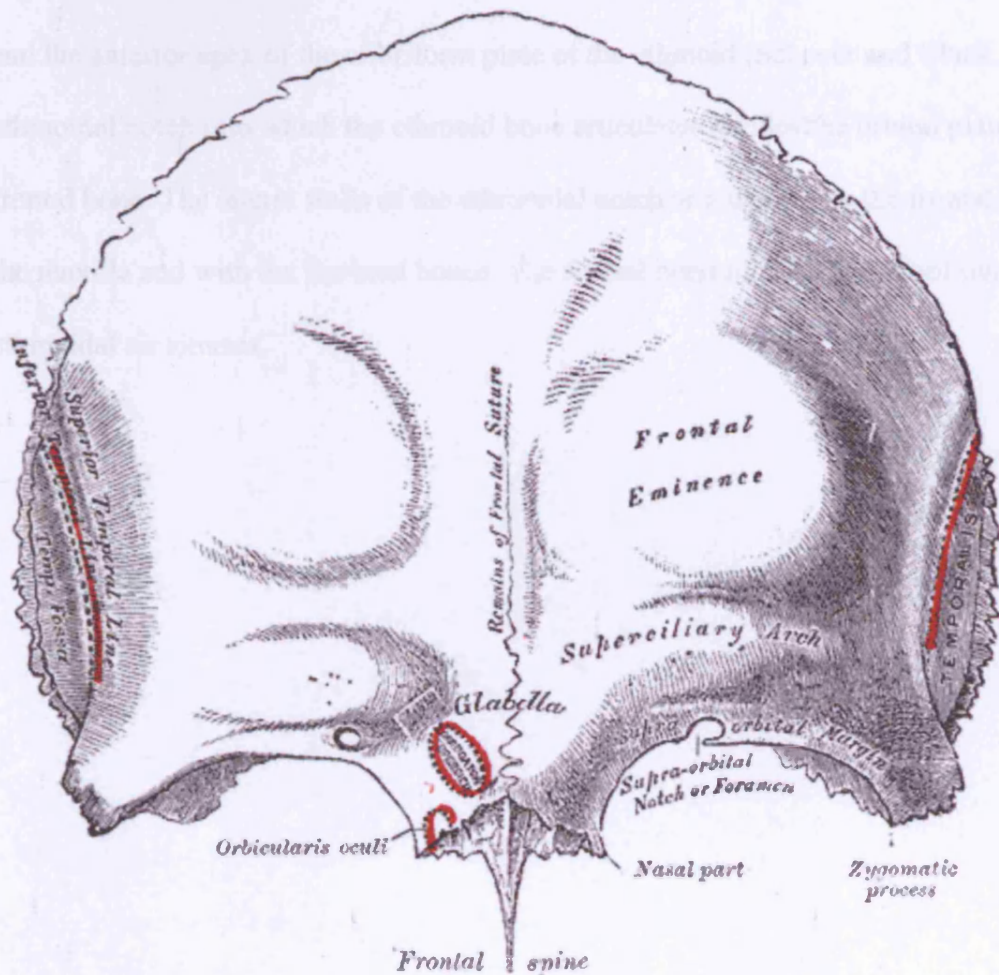


Figure 2.1. Frontal bone. External surface. From Gray, H. (1918) *Anatomy of the Human Body*, 20th ed.

Endocranial surface

The internal surface of the frontal bone is concave and burrowed by grooves of meningeal vessels and pits for arachnoid granulations (Fig. 2.2). The superior sagittal sinus forms a midline groove, which anteriorly transforms into a frontal crest. On either side of the

middle line bone, there are depressions for the convolutions of the brain, and numerous small furrows for the anterior branches of middle meningeal vessels (Gray's Anatomy, 1989). The continuation of the midline structures of the frontal bone leads to the foramen caecum. It represents a posterior-most point of the frontal bone in the mid-*sagittal* aspect and the anterior apex of the cribriform plate of the ethmoid (Scheuer and Black, 2000). An ethmoidal notch into which the ethmoid bone articulates divides the orbital plates of the frontal bone. The lateral walls of the ethmoidal notch articulate with the frontal process of the maxilla and with the lacrimal bones. The frontal bone forms a bony roof overlying the ethmoidal air sinuses.

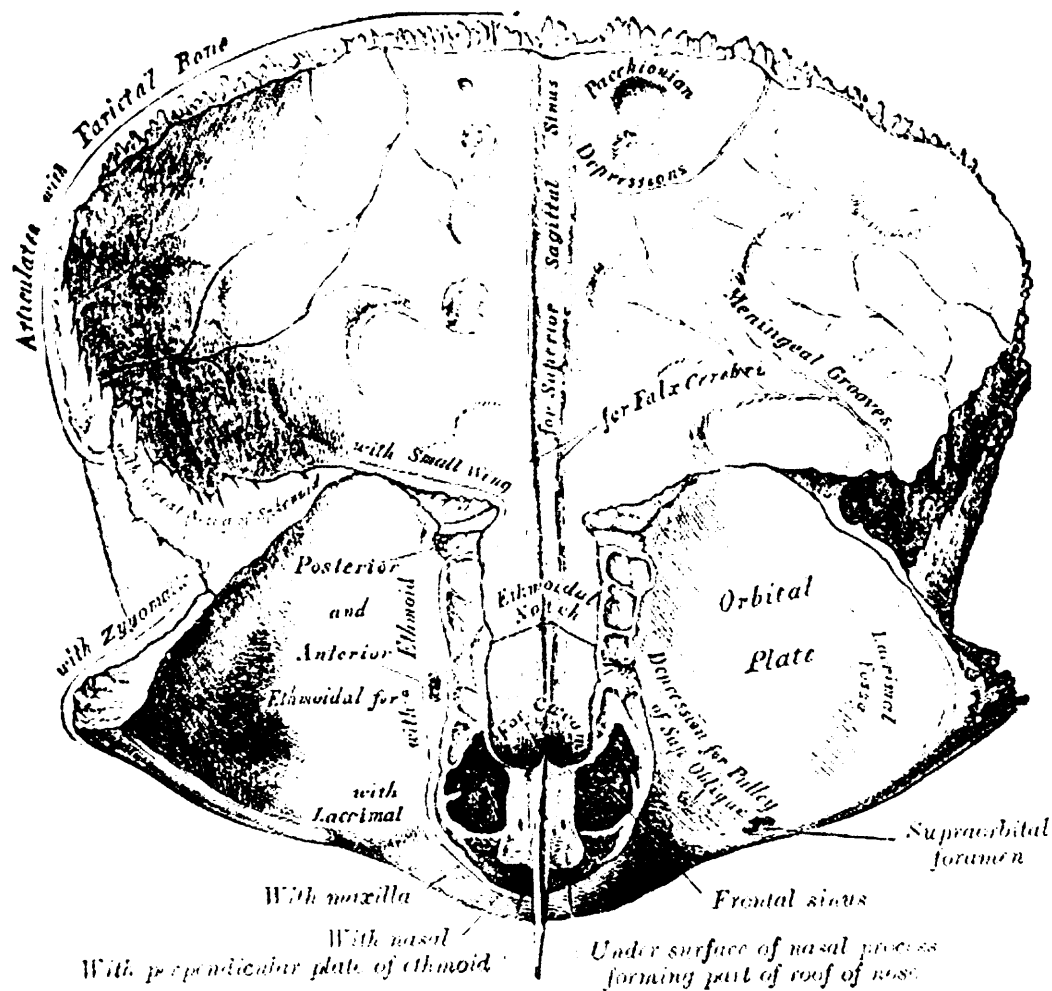


Figure 2.2. Frontal bone. Internal surface. From Gray, H. (1918).

Frontal sinuses

Behind the glabella and between anterior and posterior plates of the frontal bone lie frontal air sinuses. They are lined by a mucous membrane, and each communicates with the corresponding nasal cavity by means of a passage called the frontonasal duct (Aiello and Dean, 1990). The frontal sinuses are normally divided into a right and left chamber by a central septum. However, there is a very high level of individual variation in the number of chambers and the form of the sinuses. They may extend a considerable way between the inner and the outer tables of the frontal bone and sometimes penetrate horizontally into the orbital plates, or even into the crista galli of the ethmoid (Scheuer and Black, 2000).

Muscle attachments

Muscles temporalis insert along temporal lines of the frontal. A number of muscles of facial expression have their insertion on the frontal. *Corrugator supercilii* and *orbicularis oculi* are attached to the medial part of superciliary arches. Anterior fibres of the frontal parts of *muscles occipitofrontalis* blend with *corrugator supercilii* and *orbicularis oculi*. Posteriorly, fibres of the frontal part of *muscles occipitofrontalis* blend with *galea aponeurica*. (Van de Graaf, 1998).

Early development and ossification

Scheuer and Black (2000) present an update on the ontogeny of the skeleton in humans. Most of the information presented here is derived from this source, unless stated otherwise.

The frontal bone, together with other vault bones of the skull, develops from the mesenchyme formed by cells of the foetal neural crest. The vault of the skull appears at the end of the first foetal month as membranous neurocranium. Most of the vault bones ossify directly in this membrane. The presence of the underlying brain is necessary for the induction of ossification. As such, the frontal bone is a fully intramembraneous bone.

Unlike vault bones, bones of the cranial base and major part of the nose, including basal, lateral parts and lower squama of the occipital bone, the petromastoid parts of the temporalis, the body, the smaller wings and the medial parts of the greater wings of the sphenoid, and the ethmoid and inferior conchae derive from embryonic chondrocranium. The latter forms from embryonic mesenchyme surrounding the developing brain and primitive pharynx. This mesenchyme appears in the occipital region during the fourth week of intrauterine life and then spreads anteriorly by the beginning of the second month.

Cranial base angulation, measured at the prechordal–chordal junction by lines from nasion to sella, and sella to basion, changes rapidly during early foetal development, as reflected by the rapidly growing brain and the extension of the neck region. It flexes from about 130° in the 7-week embryo (cartilaginous stage) to $115\text{--}120^\circ$ at 10 weeks (pre-ossification stage) and then widens again to between 125° and 130° by 20 weeks as the cranial base ossifies. The prechordal cranial base increases in length and width sevenfold, whereas the posterior part grows only fivefold as these changes keep pace with the rate of development of different parts of the brain.

The basic organization of the face begins at approximately the same time as the formation of the membranous neurocranium. Most of the superficial bones develop in membrane from migrating cell populations that are derived mainly from the neural crest. However, ossification entails a complex interaction between this mesenchyme and the overlying epithelium of the facial region. These superficial bones include maxillae, palatines, nasals, lacrimals, zygomatics and the vomer. Derivatives of the pharyngeal arches contribute to the maxilla, mandible, ear ossicles, styloid process of the temporal, hyoid bone and the skeleton of the larynx.

Each half of the frontal bone ossifies from a single centre, which appears in membrane covering the anterior brain region between 6 and 7 weeks of pre-natal development. Ossification spreads as a network radiating trabeculae, at first more rapidly in the pars frontalis than in the pars orbitalis. This first burst of ossification gives rise only to part of the superciliary arch medial to the future supraorbital notch. The lateral two-thirds of the arch and the zygomatic process develop later, between 10 and 12 weeks, thus separating the orbital cavity from the temporal fossa. This process accentuates the appearance of the

separate ossification centre. A similar process occurs at the medial end of the superciliary ridge, where the orbital plate is slow to ossify and this is complete by about 13 weeks.

At birth, the frontal bone is composed of two symmetrical halves, which are separated from each other by the metopic suture. The anterosuperior angles meet the parietal bones at the diamond-shaped anterior fontanelle; 38% of fontanelles are closed by the end of the first year and 96% by 2 years. The fontanelle and its contiguous sutures may contain separate ossicles, which usually fuse with surrounding bone by the fifth year of life. Closure of the metopic suture normally takes place during the first year but completion can last until the fourth year. It starts to close just above the nasal end. In a number of individuals, which varies with the population, the suture is retained in its entirety into adult life, but many skulls show some sign of an irregular suture just above the junction with the nasal bone.

Growth pattern

After the rapid increase in chord, arc and thickness measurements, the frontal bone becomes increasingly more arched until the third year, reflecting early brain enlargement. After this time, there is a deceleration of growth leading to a flattening of the bone. The post-natal growth pattern of the frontal bone is closely correlated to the growth of two morphologically and functionally distinctive areas: neurocranium and face.

The vault and eye socket formation follow the very rapid rate of growth of the brain and eyes; 25% of their growth is reached by birth, 50% by 6 months of age, 75% by 2 years and growth is almost complete by 10 years (Sperber, 1989, cited by Scheuer and Black, 2000).

As the brain grows, the upper face grows away from the rest of the cranial base. The orbital

cavity expands anteriorly, inferiorly and laterally through drift and displacement (Moss and Young, 1960; Enlow, 1990). The growth of the frontal lobes of the brain affects the position, orientation and shape of the orbital roof, which is also the floor of the anterior cranial base.

Development of the supraorbital region is connected to the development of the facial complex. The latter is primarily correlated with the development of dentition and muscles of mastication, and is more dominant later in childhood. Thus, calvarial to facial proportions are about 8:1 at birth, 4:1 at 5 years and about 2.5:1 in adult life. The majority of facial growth (95%) is completed by the end of the adolescence growth spurt in modern humans (Farkas et al., 1992a; 1992b). After cessation of brain growth, which in modern humans occurs between 6 and 9 years of age, the orbital cavities and superstructures grow anteriorly and laterally away from the anterior cranial fossa. In humans, the upper face does not emerge from under the anterior cranial base until after the eruption of the second molars (Riolo et al., 1974; Lieberman, 2000). There is certain degree of sexual dimorphism in the pattern of the growth of the anterior neurocranium and face in modern humans, which is composed of the initial, possibly pre-natal, differences in cranial shape between sexes, differences in association between size and shape, male hypermorphosis and differences in the direction of the male and female growth trajectories (Bulygina, et al., 2006).

Growth of the frontal sinuses also influences the pattern of frontal bone development. The frontal sinus appears in foetal life as a mucosal evagination at the anterior end of the middle meatus of the nose of anterior ethmoidal cells, but does not pneumatize the frontal bone until the postnatal period. Expansion begins at the age of 3.5 years, is level with the orbital roof between 6 and 8 years and then increases slowly until puberty. The main period of

enlargement coincides with the pubertal growth spurt, the end of which is about 13 years in girls and 15 years in boys. Thus, the period of growth is shorter in girls and the mean final size is smaller than in boys. There are reports that the sinus may continue to increase well into the fourth decade of life (, cited by Scheuer and Black, 2000)Lang, 1989).

It is widely accepted that inner and outer tables of the frontal bone have different developmental trajectories (Bookstein et al., 1999b). If the inner table grows as part of the neurocranium, the outer table, including orbital plates and supraorbital region, grows together with the face, partially independent from the inner plate (as reviewed by Lieberman, 2000). This notion is highly important for an explanation of the development of the supraorbital region in primates. As is advocated by the supporters of the 'spatial relationships' hypothesis of browridge development, the latter demonstrates correlation with the degree of facial projection to the front of the neurocranium (Ravosa, 1991b; Ravosa, 1988; Lieberman, 2000). In this case, the neuro-orbital disjunction represents the distance between external and internal plates of the frontal bone. Frontal sinuses in this case most probably are a byproduct of drift of the external plate to the front and have no particular function associated with them that drives their development.

Lieberman (2000) suggests that the different growth trajectories of the inner and outer tables of the frontal bone probably account for why large browridges, when they occur, in modern humans, grow most rapidly towards the end of the adolescent growth spurt when the face reaches its adult size (Knott, 1971; Riolo et al., 1974). In non-human primates, browridges begin to form early in development as the face grows anteriorly from the neurocranium (Krogman, 1969; Shea, 1985a; Shea, 1985b; Sirianni and Swindler, 1985; Schneiderman, 1992).

As it is demonstrated above there is great amount of knowledge is amassed on the morphology of the human frontal bone and differences in the ontogenetic patterns in primate species. This circumstance provides for a good ground for comparative morphological research as is offered in the present work.

Chapter 3 Material

North-East Eurasian fossils

Relevant material from the territory of the former Soviet Union includes nine fossils, four of which are children and one, possibly, subadult.

Podkumok

The Podkumok frontal bone was found at the River Podkumok near Pyatigorsk, Caucasus in 1918. Gremyatski (1922; 1934; 1948) describes the morphology of this frontal bone as Neanderthal. Drobyshevski (2001) offers the latest interpretation of this fossil as an early Modern Human with a number of archaic features, which, however, are not sufficient to attribute this fossil to *Homo neanderthalensis sensu stricto*. Both authors agree that this frontal bone is most probably female.

Unfortunately, the geological context of this finding is not known due to the history of discovery. It was unearthed during the Pyatigorsk canalisation works during the turbulence of the Civil War in the Caucasus, which basically prevented any archaeological excavations. The finding of a Neolithic tool well above the calvaria caused disagreement in respect of the age of the fossil in Russian literature (Rentgarten, 1922; Jegorov, 1933; Gremyatski, 1934; Lunin, 1937; Alexeev, 1978). However, the Podkumok frontal bone seemed to have been covered in ochre, which provided authors of the discovery with assurance that the bone was not older than Upper Palaeolithic.

The Podkumok Calvarium is repositied in the Museum of Anthropology of the Moscow State University (11, Mokhovaya Street, Moscow 103009, Russia) (Fig. 3.1).

Skhodnya

The Skhodnya frontal bone was found in the riverbank of the River Skhodnya, near Moscow in 1936. Fortunately, the geological position of the finding was well recorded and described. Most authors agree that this frontal bone originates from a late Würm geological layer (Bader, 1952a; Sakharov, 1952).

Gremyatski (1952b) attributed this fossil to modern humans. However, he also noted a number of measurements and descriptive features that make this bone similar to more archaic forms. Gremyatski concludes that Skhodnya should belong to the group of transitional fossils, which retain some aspects of archaic morphology in a varying state. Drobyshesky's re-analysis (2001) placed this frontal bone within the sample of Upper Palaeolithic modern humans. The latter author concludes that Skhodnya is most possibly a male frontal bone due to its size and robustness.

The Skhodnya Calvarium is repositied in the Museum of Anthropology of the Moscow State University (11, Mokhovaya Street, Moscow 103009, Russia) (Fig. 3.2).

Khvalynsk

The Khvalynsk frontal bone was found at Khoroshevski Island, near the city of Khvalynsk in 1927. The history of the discovery and its geology were described by Bader (1940; 1952b). The Khvalynsk frontal bone had been partly exposed by the river current when archaeologists discovered it. It originates from a low-energy alluvial layer at the northern part of the island. This layer also contained highly mineralised bones of large mammals.

Later, it also yielded a human femur, which was claimed to contain some 'primitive' characteristics. The date of the fossil was preliminarily estimated as early Upper Palaeolithic on the basis of the fauna found in the same layer as the frontal bone.

A complete morphological description was given by Gremyatski (1952a), who placed this fragment among transitional forms between Neanderthals and modern humans, such as Podkumok and Skhodnya. Drobyshevski (2001) also found that the Khvalynsk frontal bone shares some similarities with archaic humans, but to a lesser extent than Podkumok, and, in fact, clusters better with Western Asian early modern humans from Skhul and Qafzeh and Upper Palaeolithic modern humans from Europe. The sexual affinity of Khvalynsk is unclear.

The Khvalynsk frontal bone is deposited at the Museum of Anthropology of the Moscow State University (11, Mokhovaya Street, Moscow 103009, Russia) (Fig. 3.3).

Satanay calvarium

The finding of a skull and a number of postcranial remains in Satanay Grott, Gubskiy Shelter 7, Prikuban'e, North West Caucasus, was made during excavations by V.P. Lubin and P.U. Autlev in 1975. The cultural context of the Satanay skull is most possibly Upper Palaeolithic. The first anatomical description was given by Romanova and Kharitonov (1984).

The skull is not complete: most of the face is absent (Fig. 3.4). It is rather small and gracile. Morphologically, the Satanay skull is different from both recent modern humans and Neanderthals. It is claimed to be similar to the central and eastern European Upper Palaeolithic people (Romanova and Kharitonov, 1984).

The Satanay skull is repositied in the Museum of Anthropology of the Moscow State University (11, Mokhovaya Street, Moscow 103009, Russia).

Starosel'e

Starosel'e 1 is an infant of 15–19 months, represented by a cranium, mandible with *dentes decidui* and postcranial remains. Human remains were found in a rock-shelter, near the village of Starosel'e, an eastern suburb of Bakhchisarai, Crimea, Ukraine by A.A. Formozov, during excavations in 1953 (Starosel'e 1) and 1954 (Starosel'e 2).

Starosel'e child (Fig. 3.5) was initially described by Roginski (1954). The morphology of the child is strikingly modern, and was also claimed to exhibit some Neanderthal features. Alexeev (1976) suggested that Starosel'e individuals were early modern humans who used Mousterian technology.

The remains were associated with Mousterian archaeological artefacts. Several faunal remains were dated at 41–42 ka (Gvozdover et al., 1996). However, the Mousterian origin of the Starosel'e individuals has been challenged by Marks *et al.* (1997) who claimed that human bodies, in fact, were buried deeply from a modern layer and are modern Muslim individuals. This position is criticised by specialists and contemporaries of the excavations (Alexeeva, 1997). The present work assumes a Mousterian date of the Starosel'e child until further information arises.

The repository of the Starosel'e skull is the Museum of Anthropology of the Moscow State University (11, Mokhovaya Street, Moscow 103009, Russia).

Sungir'

Sungir' is one of the richest Upper Palaeolithic sites on the territory of the former Soviet Union which has yielded human remains. Three out of eight individuals found are available for study (Fig. 3.6, photographs sited with the permission of M.B. Kozlovskaya from Kozlovskaya and Mednikova, 2000):

Sungir' 1 is a male about 55–65 years of age. The remains include a virtually complete cranium, mandible and post-cranial skeleton.

Sungir' 2 is a fairly complete child skeleton, including the skull. Most probably, this child is male and is about 12–14 years old.

Sungir' 3 is also an almost complete child skeleton and skull, most probably female and 9–10 years old.

The Sungir' finding has been continuously discussed in Russian literature from the moment of its discovery. The most recent publications are organised into a monograph (Alexeeva et al., 2000).

Sungir' represents an open site about one kilometre to the East of Vladimir, Russia. O.N. Bader discovered human remains during excavations in 1964 (Sungir' 1 and 5) and 1969 (Sungir' 2 and 3). Both sets of human remains are thought to be associated with the single occupational horizon present. Sungir' 1 was found in a grave 60–65 cm under the occupational level. It was supplied with a large number of cultural items. Sungir' 2 and 3 (two children's skeletons, richly adorned with bone ornaments) were buried together in yellow sandy loam below the buried soil and 50 cm below the occupational horizon (Tsetlin, 1965; Sukachev et al., 1966).

The archaeological context of the finding was diagnosed as Upper Palaeolithic of 'Kostenki-Sungir' variation (Sukachev *et al.*, 1966). Dolukhanov *et al.* (2001) site calibrated date estimate for the Sungir' site as 29,000+/-922 calibrated years BP, whereas Sulerzhitski *et al.* (2000) provide list several ages for the estimates from bone and coal from the burials (including direct dates) which on average amount to about 23,000 radiocarbon years BP.

Repository of fossils: Laboratory of Reconstruction, Institute of Anthropology and Ethnology of the Russian Academy of Sciences.

Teshik-Tash

Teshik-Tash finding contains a complete cranium and a number of fragmentary postcranial bones of a Neanderthal from Uzbekistan, Central Asia. A number of other sites from the territory of the former Soviet Union yielded Neanderthal remains: postcranial remains of an infant and an adult from the Kiik-Koba, fragments of an adult occipital, a sub-adult mandible and metacarpals and phalanges from Zaskal'naya (Crimea); bones of a baby Neanderthal from the Mesmaiskaya Cave, fragments from a mandible from the Barakay Cave and, may be, fragments from Monasheskaya cave (Northern Caucasus). Hominin remains are also known from other Central Asian sites, such as Obi-Rakhmat, Anguilak and Okladnikov Cave. These findings are quite fragmentary and, although some archaic features have been detected for them, their taxonomic position is still questionable (Marks *et al.*, in press; Viola *et al.*, 2006).

The Teshik-Tash cave is located 125 km to the south of Samarkand in Southern Uzbekistan. A.P. Okladnikov found human remains here in 1938, after which this finding was widely discussed in paleoanthropological literature. A meticulous study of the Teshik-

Tash geology, archaeology and human remains has been published in a monograph by Gremyatski and Nesturkh (1949).

Teshik Tash 1 is a male child 8–10 years of age. The cranium has been reconstructed from a number of pieces, which, however, provided for a relatively good match (Fig 3.7).

The repository of Teshik-Tash human remains is the Museum of Anthropology of the Moscow State University (11, Mokhovaya Street, Moscow 103009, Russia).



Figure 3.1. Podkumok calvarium.



Figure 3.2. Skhodnya calvarium.



Figure 3.3. Khvalynsk calvarium.

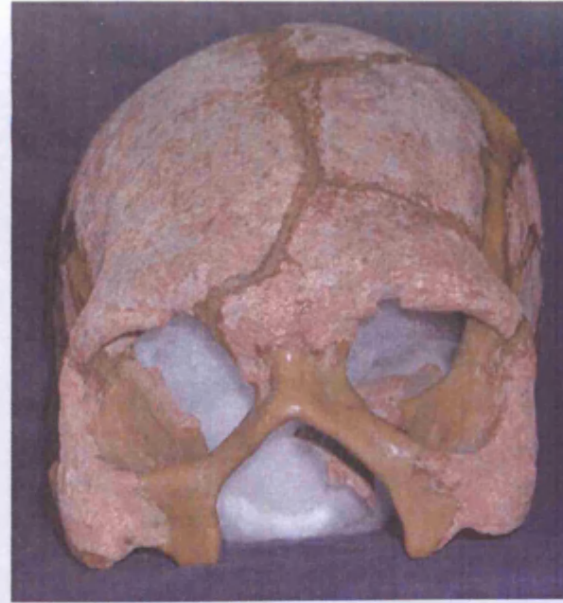
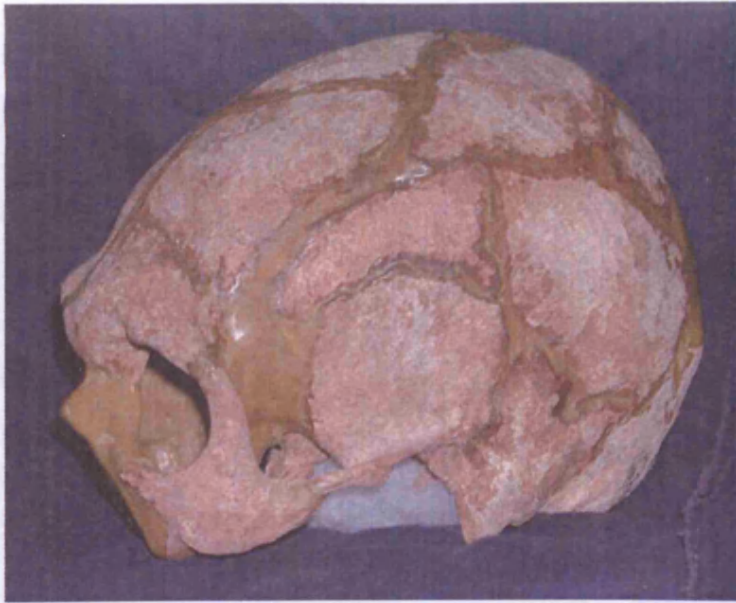


Figure 3.4. Satanay calvarium.

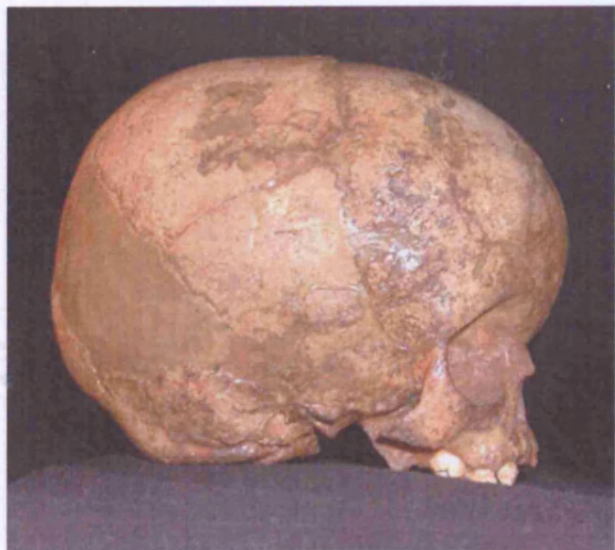


Figure 3.5. Starosel'e cranium.

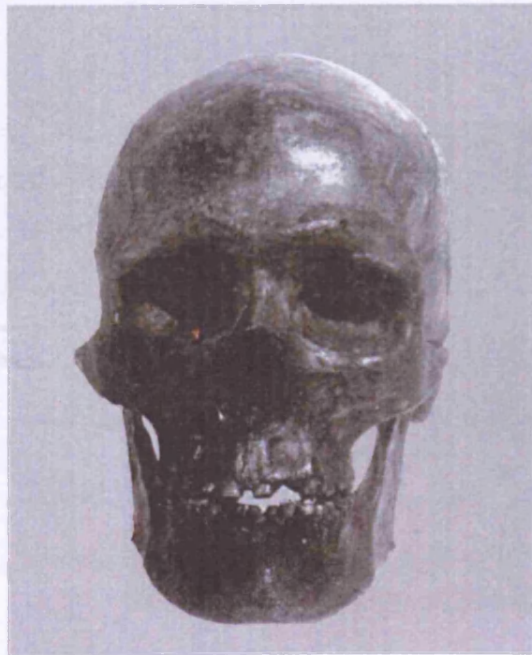
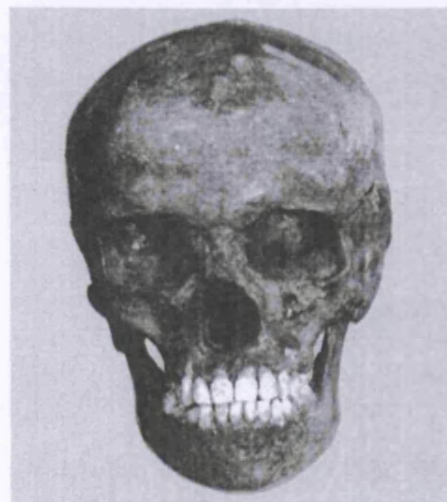


Figure 3.6a. Sungir 1.

Figure 3.6b. Sungir 2.



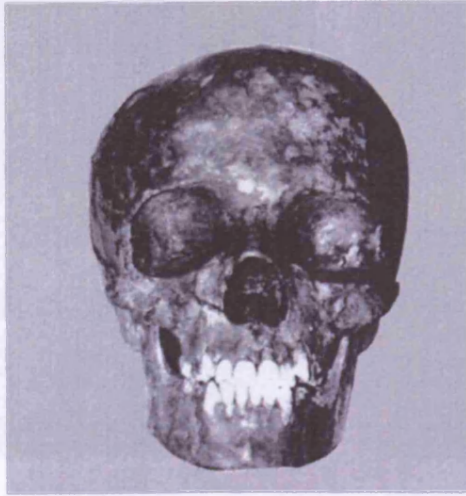


Figure 3.6c. Sungir 3.

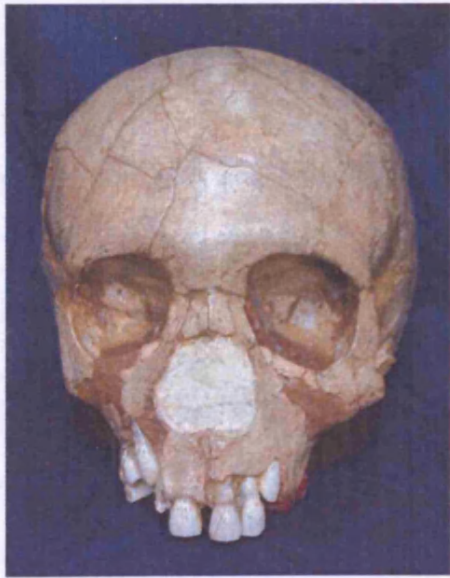


Figure 3.7. Teshik-Tash cranium

Modern populations

Modern comparative material has been chosen to encompass the wide geographical variation of modern humans. However, the availability of collections and time-consuming character of the data collection techniques (see below) put certain limitations on the kind of populations as well as on the number of individuals measured. Given that the inter-population variation is not the subject of the present work, it has been considered sufficient to have only a few individuals from each population as long as they included males, females and juveniles when available. In total, 161 individuals representing nine modern populations around the world were measured (Table 3.1). Only complete undistorted skulls were used. Both adult and juvenile data have been collected and utilized in corresponding parts of the comparative analysis.

Table 3.1 Comparative sample of the recent modern human populations.

<i>Group</i>	<i>Deposited</i>	<i>Composition</i>	<i>Origin and time</i>
Europe			
British	Duckworth Laboratory, Cambridge, UK (16 individuals)	5 males, 5 females and 6 juveniles	Brandon, Suffolk, probably Roman times
Africa			
Egyptians	Duckworth Laboratory, Cambridge, UK (23 individuals)	8 males, 8 females and 7 juveniles	Gizeh, time of the 25-30 th dynasty (19 individuals); Naqada, pre-dynastic (4 individuals)
Teita	Duckworth Laboratory, Cambridge, UK (20 individuals)	10 males, 7 females and 3 juveniles	Kenya, modern times
Asia			

Andamanese	Natural History Museum, London, UK (12 individuals)	5 males, 5 females and 2 juveniles	Andaman islands, modern times
Buryat	Moscow University Museum of Anthropology, Moscow, Russia (16 individuals)	6 males, 7 females and 3 juveniles	A number of locations near lake Baikal, modern times: Goremyka (North Pribaikelie) (3 individuals); Troitsko-Savski Aimak (4 individuals); Tunka and other sites in Zabaikalie region (9 individuals)
Chukcha	Moscow University Museum of Anthropology, Moscow, Russia (16 individuals)	6 females, 6 males and 4 juveniles	Chukotka peninsula, modern times: the site locations include Yandagay (10 individuals), Nunyamo (5 individuals), Uelen (1 individual)
Eskimo	Moscow University Museum of Anthropology, Moscow, Russia (13 individuals)	7 males and 6 females	Naukan, Chukotka peninsula, modern times
<hr/> America <hr/>			
Santa Cruz	Natural History Museum, London, UK (16 individuals)	5 males, 7 females and 4 juveniles	Chumash Indians from Santa Cruz island, one of the Channel islands off the coast of California, modern times
<hr/> Australia <hr/>			
Australians	Natural History Museum, London, UK (13 individuals) and Duckworth Laboratory, Cambridge, UK (4 individuals)	Australian Aborigines: 6 males, 6 females and 5 juveniles	New South Wales, modern times – 8 individuals; South Australia, modern times – 4 individuals; Western Australia, modern times – 3 individuals; Queensland, modern times – 1 individual, unknown – 1 individual

Fossils

The comparative sample of fossils represents Western European (Classical) Neanderthals, eastern Neanderthals, Upper Palaeolithic modern humans from Europe and early modern humans from Western Asia, as well as a sample of archaic African forms (Table 3.2). The availability of the fossil data had a significant influence on the composition of the comparative sample. Preference was given to original fossils with largely complete frontal

bones. Some casts were introduced when originals were not available but inclusion of the particular fossil was deemed relevant to the subject of the research.

Table 3.2 Comparative sample of fossils.

<i>Name</i>	<i>Geographical origin</i>	<i>Group</i>	<i>Deposited</i>
<u>Europe</u>			
Pech de l'Aze	France	Neanderthal	Musee de l'Homme, Paris
La Chapelle aux Saints	France	Neanderthal	Musee de l'Homme, Paris
La Ferrassie	France	Neanderthal	Musee de l'Homme, Paris
La Quina	France	Neanderthal	Musee de l'Homme, Paris
Le Moustier	France	Neanderthal	Museum für Vor- and Frühgeschichte, Berlin
Neanderthal	Germany	Neanderthal	Rheinisches Ladesmuseum, Bonn
Engis	Belgium	Neanderthal	University of Liege
Gibraltar 1	Gibraltar	Neanderthal	Natural History Museum, London
Gibraltar 2	Gibraltar	Neanderthal	Natural History Museum, London
Šal'a	Slovak Republic	Neanderthal	Slovenske Narodne Muzeum, Bratislava
Abri Pataud	France	UP modern human	Musee de l'Homme, Paris
Aubert	France	UP modern human	Musee de l'Homme, Paris
Cro-Magnon 1	France	UP modern human	Musee de l'Homme, Paris
Cro-Magnon 2	France	UP modern human	Musee de l'Homme, Paris
Cro-Magnon 3	France	UP modern human	Musee de l'Homme, Paris
DV 3*	Czech Republic	UP modern human	Dolni Vestonice museum base
DV 13	Czech Republic	UP modern human	Dolni Vestonice museum base

DV 14	Czech Republic	UP modern human	Dolni Vestoniče museum base
DV 15	Czech Republic	UP modern human	Dolni Vestoniče museum base
DV 16	Czech Republic	UP modern human	Dolni Vestoniče museum base
Pavlov	Czech Republic	UP modern human	Dolni Vestoniče museum base
Mladeč 1	Czech Republic	UP modern human	Natural History Museum, Vienna
Mladeč 2	Czech Republic	UP modern human	Natural History Museum, Vienna
Mladeč juvenile	Czech Republic	UP modern human	Natural History Museum, Vienna
Predmosti 3*	Czech Republic	UP modern human	Dolni Vestoniče museum base
<hr/>			
<u>Western Asia</u>			
Amud*	Israel	Neanderthal	Musee de l'Homme, Paris
Shanidar 1*	Iraq	Neanderthal	Musee de l'Homme, Paris
Zuttiyeh*	Israel	Early archaic modern human	Musee de l'Homme, Paris
Tabun	Israel	Neanderthal	Natural History Museum, London
Qafzeh 1*	Israel	Archaic modern human	Musee de l'Homme, Paris
Qafzeh 2*	Israel	Archaic modern human	Musee de l'Homme, Paris
Qafzeh 6*	Israel	Archaic modern human	Musee de l'Homme, Paris
Skhul V*	Israel	Archaic modern human	University College London, Anthropology Department
Skhul IX	Israel	Archaic modern human	Natural History Museum, London
<hr/>			
<u>Africa</u>			
Broken Hill	Zambia	<i>Homo heidelbergensis</i>	Natural History Museum, London

Singa	Sudan	Archaic modern human	Natural History Museum, London
<hr/>			
Australia			
Kanalda	Australia	Holocene modern human	Natural History Museum, London
<hr/>			

* Measurements are taken on casts.

Chapter 4 Methods

Data procurement

Age estimation

All immature individuals in this study were screened for their biological age. As only cranial material was available for most individuals in the screened collections, dental ‘ageing’ methods were chosen for age detection. A number of methods are available for age estimates of teeth, including methods based on incremental lines/perikymata counting (Boyde, 1963; Dean and Beynon, 1989; 1991), tooth height measurements (Israel and Lewis, 1971; Liversidge et al., 1993; Liversidge and Molleson, 1999), or developmental status estimates for each separate tooth (Moorrees et al., 1963a; Moorrees et al., 1963b; Demirjian et al., 1973), which for technical reasons are difficult to apply to the archaeological material from museum collections. Unlike the listed methods, Ubelaker’s (1989) adaptation of the standard of Schour and Massler (1941) may be preferable for use on osteological collections as it avoids costly methods such as obtaining radiographs for a large number of individuals or using destructive techniques such as teeth sectioning. Ubelaker’s standards refer to the formation of the teeth and the sequence of eruption of teeth, which in most cases are easy to assess on fragmentary archaeological material. The standards represent 21 developmental stages, two of which are inter-uterine. Each stage is assigned to an age interval spanning from 4 months in infancy to 6 years in adolescence. The average age of the stage can be recorded for each individual if used in statistical analysis.

Although it has been developed for use on non-white populations, the technique contains data from two different sources, i.e. American Indians for permanent dentition and white non-Indian American children for deciduous dentition. Hillson (1986; 1996) summarises a number of studies on population differences in eruption pattern and suggests that the maximum differences between populations are unlikely to be more than 6 months – fitting within the expected range of individual variation. However, according to the test by Strand-Vidarsdottir (1999), the standards perform better on white populations of European descent than on African American populations. African American children tend to have advanced tooth development compared to other populations with an average discrepancy of 1.13 years compared with the chronological age. A French Caucasian sample, in comparison, gives only 0.58 years discrepancy with the chronological age (Strand-Vidarsdottir, 1999).

On the individual level, the standards are less precise for age assessment in adolescence mainly due to the large variation in the development of the third molars (Hillson, 1986). Also, after eruption of the second molar (12 years \pm 2.5 years) and until the eruption of the third molar (about 21 years), more discrepancies may be expected on the archaeological material where it is impossible to assess third molar development without radiographs (Strand-Vidarsdottir, 1999).

In the absence of matching tables for different populations, Ubelaker's standards are used for all modern populations involved in the present work. Given the expected differences in the pattern of teeth development in different populations and between sexes, the dental age estimation is treated as an approximate estimate of biological development stage. This approach may be acceptable given that the present work does not attempt to establish ontogenetic differences between modern populations.

The development stage of each tooth present was recorded by visual assessment of the teeth *in situ* or of the teeth that were coming loose of the alveolar socket. It was sometimes possible to observe unerupted teeth, as well as tooth roots, through the damaged alveolar surfaces. In some cases, when teeth were absent from the sockets, a relatively precise judgement of root formation could be made on the basis of the shape of the crypt. A general developmental stage of the individual was estimated on the basis of information on all available teeth and recorded as the mean age of the stage following Ubelaker (1989). Individuals with the second molar fully in occlusion and its root formed (when assessable) whose third molar was still absent were assigned the age of 15. Adult individuals were identified by fusion of the sphenooccipital synchondrosis regardless of the presence of the third molar. In cases where the sphenooccipital synchondrosis was not fused but the third molar was coming into occlusion, individuals were attributed to a subadult group and assigned a tentative age of 18 years for the purpose of statistical analysis.

Sex determination

Sex determination has been used for the purpose of building modern comparative sample. Only a few individuals from the modern collections were of known sex. Most of the adult individuals were sexed on the basis of aspects of adult morphology that are useful to determine sex, i.e. the development of the nuchal crest, mastoid processes, supra-orbital margins, supra-orbital ridge/ glabella, and mental eminence, given in Buikstra and Ubelaker (1994). Whenever possible, several individuals from a population were compared following White and Folkens (2000). When choosing individuals to measure, preference was given to individuals at the extremes of the range of population variation whose sexing was less

questionable. This biased choice of individuals from a population is intended to achieve maximum variation and therefore is not used for investigation of sexual dimorphism. No sexing was attempted on fossil material. Information about the possible sexual affinity of each fossil was obtained from the relevant literature where available.

‘Traditional’ inter-landmark measurements

Two types of measurement were collected for each individual in the study: traditional inter-landmark distances and three-dimensional landmark coordinates. Inter-landmark measurement data included distances and angles following Howells (1973) and Martin (Knussmann, 1999) (Table 4.1). The majority of inter-landmark measurements in present work were calculated from the 3D data with a help of formulas in Excel (© Microsoft Corporation). However, Minimum frontal breadth and Maximum frontal breadth were taken with the help of sliding callipers on the skulls due to the method of their collection unattached to particular cranial landmarks identifiable before the measurement is taken. Minimum frontal breadth was also calculated as a distance between two frontotemporale landmarks.

Table 4.1 Inter-landmark measurements included in the study.

<i>Measurement</i>	<i>Notation by Howells (1973)</i>	<i>notation by Martin (Knussman, 1999)</i>	<i>Description</i>
Minimum frontal breadth		9	The minimum breadth across the frontal in the area of the maximum constriction above orbits (frontotemporale-frontotemporale breadth)
Maximum frontal breadth	XFB	10	The maximum breadth at the coronal suture perpendicular to the medial plane
Frontal sagittal arc	–	26	The length of the sagittal arc between nasion and bregma
Glabella-bregma arc	–	26a	The length of the sagittal arc between glabella and bregma
Frontal sagittal chord	FRC	29	Direct distance from nasion to bregma, taken in the midplane and at the external surface
Glabella-bregma chord	–	29d	Direct distance from glabella to bregma, taken in the midplane and at the external surface
Nasion-bregma subtense	FRS	29b	The maximum height of the curvature of the frontal above nasion-bregma chord
Glabella-bregma subtense	–	29e	The maximum height of the curvature of the frontal above glabella-bregma chord
Nasion-subtense fraction	FRF	29c	The distance along the nasion-bregma chord recovered from nasion, at which the nasion-bregma, or frontal, subtense falls
Glabella-subtense fraction	–	29f	The distance along the glabella-bregma chord recovered from glabella, at which the glabella-bregma, or frontal, subtense falls
Frontal angle	FRA	32(5)	In the sagittal plane, the angle underlying the curvature of the frontal bone at its maximum height above the frontal chord: computed from nasion-bregma chord, nasion-bregma subtense and nasion-subtense fraction
Frontal angle from glabella	–	32(c)	In the sagittal plane, the angle underlying the curvature of the frontal bone at its maximum height above the frontal chord: computed from glabella-bregma chord, glabella-bregma subtense and glabella-subtense fraction
Outer biorbital breadth	–	43	The breadth across the frontal bone taken between outer aspects of zygomatic processes in the area of fronto-zygomatic suture
Bifrontal breadth	FMB	43a	The breadth across the frontal bone between frontomale

			anterior on each side, i.e. the most anterior point on the fronto-malar suture
Nasion-frontal subtense	NAS	43b	The subtense from nasion to the bifrontal breadth
Nasion-frontal angle)	NFA	77a	The angle at nasion whose two sides reach from their point to frontomolare, left and right: computed from bifrontal chord and nasion subtense
Interorbital breadth	DKB	49a	The breadth across the nasal space from dacrion to dacrion
Anterior interorbital breadth	–	50	The breadth across the nasal space between maxillofrontale on either side
Dacrion subtense	DKS	44c	The mean subtense from dacrion (average of two sides) to the biorbital breadth
Bistefanoid breadth	STB	10b	Breadth between the intersection on either side, of the coronal suture and the inferior temporal line marking the origin of the temporal muscle (the stephanion point)
Sphenion-sphenion	–	–	The breadth of the bone between sphenions on either side

The potential advantage of inter-landmark measurements is their direct compatibility with a large amount of craniometric data collected and published by researchers in the past. Inter-landmark measurements proved to have good discriminative powers between populations and/or between fossil hominins in a number of analyses, such as Howells (1973; 1989) and Lahr (1996). However, inter-landmark measurements (not including angles) are usually highly correlated with size (Bookstein et al., 1985). Therefore, shape exploration frequently involves use of size correction methods (Sundberg, 1989; Jungers et al., 1995b), which give slightly different results. Until now, there has been little agreement on which method should be used. Most importantly, the same set of distances can be obtained from different shapes. For example, if the maximum length and width are taken on oval and teardrop shapes, both objects may have the same heights and widths but be completely different in shape (Adams et al., 2004). Finally, the geometric relationships are usually lost with inter-landmark data. It is not possible to re-create a graphical representation of shape, unless distances were carefully selected to fix the relative position of every point up to a

reflection. It normally involves either measurement of the angle between each two distances or measuring distances between each of the three points (Slice, 2005).

Three-dimensional landmarks and semi-landmarks

The landmark method has been developed in order to solve problems of shape analysis imposed by inter-landmark measurements (Slice, 2005). The essence of landmark collection is in registering two- or three-dimensional Cartesian coordinates for each point of interest on a specimen. The choice of such points is dictated by what is being investigated. Frequently, these are the same anatomical landmarks that are routinely used in traditional inter-landmark morphometrics. However, precision of identification and repeatability of landmarks on different samples are an important issue of homology given that all the statistical methods require homologous data for analysis. Bookstein (1991) proposed a classification of landmarks into three types. Type 1 landmarks are identified with respect to discrete juxtaposition of tissues, such as triple points of suture intersections. Type 2 are curvature maxima associated with local structures usually with biomechanical implications, and Type 3 landmarks are extreme points, defined with respect to some distant structure. Type 1 and 2 landmarks have all three of their dimensions biologically informative as they are defined with respect to the local morphology. They are also easily repeatable across the sample with reasonable precision. Type 3 landmarks are 'deficient' as they contain meaningful information only in line with the remote defining structure. Variation orthogonal to this component is largely meaningless (Bookstein, 1991). The first two types of landmarks have been extensively used in geometric morphometric studies for the past decades. An unsolved problem of landmark usage has, until recently, been the inability to

describe curves and surfaces. Other methods have been developed, such as Fourier analysis (Rohlf, 1990), and successfully applied to curve description (see, for example, Anton, 2003), which, however, excluded combination with landmark methodology (Slice, 2005). A breakthrough resolution of this problem came with the development of the theory of Type 3 or, as they are now called, *semi-landmarks*. Bookstein (1991) proposed to eliminate the confounding influence of the deficient coordinates by computing them solely using the part of the data that was not deficient. In other words, these coordinates are treated as missing and estimated, all at once, in order to minimise the net bending energy of the dataset as a whole around its own Procrustes average (see below) (Gunz et al., 2005). This concept has been refined and repeatedly used in a number of papers (Bookstein et al., 1999a; Gunz et al., 2004b; Mitteroecker et al., 2004; Neubauer et al., 2004; Schaefer et al., 2004; 2006; Mitteroecker et al., 2005a; 2005b; Gunz and Harvati, 2006; Bulygina et al., 2006).

Major mathematical tools in geometric morphometrics

Thin plate spline function and its application to semi-landmarks

The thin-plate spline function (Bookstein, 1989; 1991) has been initially adapted in morphometrics as a means to solve a problem of expression of shape differences between two specimens. This single function, on one hand, helps to integrate information about the relative location of all landmarks of one specimen and, on the other hand, maps the Cartesian space of one specimen into that of another (Slice, 2005). The resulting picture represents a grid (Thompson, 1942) where landmarks of one specimen (the template) can be imagined to be ‘attached’ to it. The grid deforms in such a way that the landmarks of the template superimpose onto the landmarks of the second specimen (the target). The amount

of deformation at each landmark is calculated to minimise its bending energy of the grid as if the bending was applied to an infinitely thin metal plate. The formula further interpolates bending energy onto the neighbouring grid intersections so that the resulting picture represents the minimum of total deformation possible in this superimposition. This property of minimisation of the bending energy of the thin-plate spline function has allowed it to be applied as a criterion for the optimization of semi-landmarks (Bookstein, 1991; 1997; Gunz et al., 2005; Gunz, 2005). The semi-landmarks are allowed to slide along tangent vectors to the curve iteratively until the bending energy between a template and a target form is minimal. In the extension of formalism to surfaces, the semi-landmarks are allowed to slide on tangent planes instead of the tangent vectors. The mathematical formalization is developed by Bookstein (1991, 1997), Gunz *et al.* (2005) and Gunz (2005).

Procrustes superimposition

The Procrustes superimposition method has recently become a standard approach in geometric morphometrics. It allows a comparison between shapes of different size, where the nature of landmark data also imposes problems of different location and orientation of the samples in space. Recent formalisation of the Procrustes superimposition in application to the anthropological data is presented in Goodall (1991), Small (1996), Rohlf and Slice (1990) and Dryden and Mardia (1998). Procrustes superimposition is a least-squares method that estimates the parameters for location and orientation minimising the sum of squared distances between corresponding points on two configurations (Slice, 2005). All specimens are scaled to the unit size, for example, by removing the *centroid size* from each specimen. The centroid size for each specimen is calculated as the square root of the sum of the squared Euclidian distances between each of the landmarks and the mean of all

landmark coordinates. The square root of the sum of squared coordinate differences after superimposition is a measure of the shape differences between configurations (Slice, 2005). Generalized Procrustes Superimposition, used here, is an iterative process where, in a sample of a number of individuals, any single specimen is initially selected as the reference. All of the configurations of the sample are fitted to that reference, and then the new mean is computed as an arithmetic average location of the individual landmarks in the sample and scaled to the unit centroid size. The process is repeated, fitting the sample to the new estimate, producing monotonically decreasing sum-of-squared deviations of the sample configurations around the estimated mean (Gower, 1975, cited by Slice, 2005). The procedure is terminated when the change in mean estimate from one iteration to the next is deemed negligible.

Procedure for acquisition of the 3D data

The procedure involved two stages: i) digitising landmarks, curves and surfaces with the help of a Microscribe (Tab.4.2); ii) mathematical generation of semi-landmarks on the curves and the surface of each individual performed in MATHEMATICA. In application to the curves in two or three-dimensional space or surfaces, the same number of semilandmarks are obtained in the same order along a curve or a surface on a number of specimens. It is important that the semilandmarks are collected between two or more fixed landmarks, which delimit their positions (Gunz et al., 2005). With the help of an algorithm based on the thin plate spline function (see below), all semilandmarks are slid along tangents to the curve or surface until the bending energy between a template and a target form is minimal (Gunz et al., 2005). In a large sample of individuals, several iterations

result in the best optimised positions of semilandmarks that can be deemed geometrically homologous across the sample (Bookstein, 1997, Gunz et al., 2005).

Table 4.2 3D data collection

	<i>raw data</i>	<i>data after mathematical transformation</i>
Fixed landmarks	bregma	the same – 19 semilandmarks
	glabella	
	nasion	
	stephanion left	
	stephanion right	
	frontotemporale left	
	frontotemporale right	
	sphenion left	
	sphenion right	
	dacriion left	
	dacriion right	
	frontomalare anterior left	
	frontomalare anterior right	
	frontomalare orbitale left	
	frontomalare orbitale right	
	frontomalare temporale left	
	frontomalare temporale right	
Curves	maxillofrontale left	sagittal - 10 semilandmarks
	maxillofrontale right	
	sagittal (between br and na)	sagittal - 10 semilandmarks
	temporal left (between stephanion left and frontomalaretemporale left)	temporal left – 4 semilandmarks
	temporal right (between stephanion right and frontomalaretemporale right)	temporal right – 4 semilandmarks

	outline	outline -36 semilandmarks
	Raw points on curves were digitised in the same order on all individuals and were more numerous than the expected final number of points:	In total – 52 semilandmarks
Surface	maximum amount of points feasibly possible was digitized (normally between 2500 and 3000 raw points on each individuals)	153 semilandmarks

The raw Microscribe data for curves and surfaces has an extensive character, following recommendations in Gunz *et al.* (2005). For example, the number of points collected from the frontal bone surface of one individual ranges from 2500 to 3000. The protocol for further mathematical generation of semi-landmarks is given by Gunz et al. (2005) and involves the following steps:

1. An initial reference mesh of surface semi-landmarks is generated by thinning the point cloud of the surface taken from the frontal bone of the first individual in the modern sample in the program Metric Base. The mesh is further perfected by the manual addition of the original points in places where thinning created large gaps or where it was deemed necessary on the basis of the research question.
2. Further steps are performed on all data simultaneously: semi-landmarks are generated on the curves by a) fitting a cubic spline to the points on each curve between two fixed landmarks; and b) re-sampling a fixed number of equidistant semi-landmarks from the functions.
3. Semi-landmarks on the surface are generated by warping the mesh onto each specimen's landmarks and projecting the received 'loose hats' onto the surface of the specimen to receive corresponding surface semi-landmarks.

4. The last step involves sliding semi-landmarks along tangent vectors for the curves and tangent surfaces for the surfaces of the frontal bone following the basic algorithm in Gunz *et al.* (2005):

- Relaxing all specimens against the first specimen;
- Computing the Procrustes average configuration;
- Relaxing all specimens against the Procrustes average.

In total, 19 landmarks and 215 semi-landmarks (52 on curves and 163 on surface), have been obtained from frontal bones of each individual (Tab.3.2). Step 4 was repeated twice: first only for the modern data, which allowed the construction of the consensus shapes for adults and children, which were later used in reconstruction (see below), and then for the whole dataset, which included both modern and fossil samples after reconstruction.

Quantitative reconstruction

Fossil material is frequently damaged, distorted or incomplete. Although many of the fossils used in the present work had complete or almost complete frontals, a considerable number of them are missing some of the landmarks or semi-landmarks due to damage. There are two standard strategies to deal with the missing data in statistics: i) cases or variables with missing values are deleted from the dataset, and ii) missing values are substituted by estimates based on complete cases. In order to maximise the amount of data available for the analysis, a certain amount of reconstruction was necessary for several fossils in the present work. The appeal of the virtual reconstruction is in the possibility of

making alterations to the virtual fossil, whether it exists in a high-resolution CT scan version or a Microscribe generated set of landmarks, without actually imposing any changes to the original.

An opportunity to reconstruct shapes in 3D with mathematical precision has arisen with the development of the geometric morphometrics toolkit. Gunz *et al* (2005) and Gunz (2005) present two methods of reconstruction of shapes in 3D. One of them, *geometric reconstruction*, is based on the information contained within the shape itself and employs properties of the thin-plate spline function. The second method, *statistical reconstruction*, is based on multiple multivariate regression formulae that can be derived from a sample of complete shapes on the assumption of correlation of all landmark locations of a specimen. These two methods of reconstruction give results that are very similar, although not identical, and converge in the case where forms are represented by a high number of landmarks and semi-landmarks (Gunz, 2005).

Gunz *et al* (2004a) investigate the properties of statistical and geometric reconstruction and compare them to the method of mean substitution of the missing data. In the mean substitution, missing entries are filled in by the value of the mean of non-missing entries over the full data set. Gunz *et al.* (2004a) note, however, that when data are Cartesian coordinates or shape coordinates this procedure makes no sense either as statistics or as a science. These authors carry out a test using a dataset of 388 anatomical landmarks and semi-landmarks on 52 complete *Homo sapiens* cranial by deliberately deleting regions of landmarks and then estimating the missing data with the help of the three methods mentioned above. The estimations are then compared with the originals and the total error is calculated. Gunz *et al.* (2004a) show that the mean substitution method performs the

worst, whereas the statistical reconstruction by regression is always better than the thin plate spline warping. The latter works best if small areas of relatively smooth surfaces are estimated. However, in the case of both, regression and geometric reconstruction, the accuracy of estimation is sufficiently close to the precision of measurement, which is not the case for the method of the mean substitutions.

The underlying assumptions of the methods of geometric and statistical reconstructions have different effects to the following analysis of the reconstructed shape. For instance, statistical reconstruction exploits the information present in the reference population. Therefore, any procedure that involves a covariance matrix (i.e. regression, principal components or singular warps) will have these relationships overfitted, i.e. the results will be so close to the sample that they would not generalise to other samples (Bookstein et al., 2003; Gunz et al., 2004a; Gunz, 2005).

This property of the statistical reconstruction made it unsuitable for the reconstruction of the fossils in the present work because the generated data were intended for use in statistical analysis. Gunz (2005) recommends to use geometric reconstruction in this case. The prediction of the missing parts of a single specimen may be based on its own geometric properties, such as continuity information of curvature. Thin plate spline (TPS) interpolation allows one to map a complete reference specimen to the specimen with missing landmarks based only on the subset of landmarks that are not missing (Gunz, 2005). The reference specimen may be a Procrustes average of all complete cases or a single specimen that matches the specimen with missing data in some other variables like age, sex or species. It is also important to note that the spline interpolation of the geometric reconstruction performs best when the missing information is smooth, such as in parts of

the neurocranium. Both requirements are met in the present work because the frontal bone has a relatively smooth morphology and it was possible to generate references for reconstruction as Procrustes average for adults and children separately.

The protocol for the reconstruction of the fossils follows the suggestion by Gunz (2005) to combine the step of missing data estimation with a thin plate spline relaxation of the available semi-landmarks against the reference specimen and is performed in

MATHEMATICA:

1. Assessment of the missing data for one fossil;
2. Manual distribution of the existing semi-landmarks on the outlines (i.e. choice of an appropriate number of approximately equally spaced semi-landmarks from the raw-data points keeping in mind the sequence number of each preserved landmark and semilandmark);
3. Warping the reference shape (i.e. all landmarks and semi-landmarks on outlines and the surface) onto the existing landmarks and semi-landmarks of the fossil;
4. Projection of the warped landmarks and semi-landmarks onto the surface of the original fossil.
5. Sliding of all semi-landmarks of the complete sample, including fossils and moderns, following the sliding semi-landmarks protocol described above.

In this protocol, the complete number of landmarks and semi-landmarks is present at step three. The positions of landmarks are corrected in accordance with the surface of the fossil

in step four. Step five helps reaching geometric homology of semilandmarks across all specimens.

This method allows the reconstruction of both missing semi-landmarks and landmarks with fair precision if the missing regions are in close proximity to actually observed landmarks and semi-landmarks. According to Gunz (2005), point prediction using TPS grid is designed to be very local: if preserved landmarks do not bend the spline near the missing landmarks, e.g. if landmarks on the occipital are estimated when only facial landmarks are known, then the grid is almost square resulting in a simple substitution of the missing points by the reference data.

Generation of the semi-landmarks for the complete fossils was performed following the protocol described above for the modern sample but using either adult or child consensus shapes as the mesh reference for each fossil separately.

Statistical analysis

This section provides for a brief description of the methods used for statistical analysis of the data in the present work. Protocols of their application are supplied at each analytical step in the Results chapter.

Principal components and Relative Warps

Principal components for the inter-landmark data and Relative Warps for the 3D data serve one and the same goal: a reduction of the raw information in the whole dataset and the hierarchical organisation of it. Principal components explain the variance-covariance

structure of a set of variables through a few linear combinations of these variables.

Although the total number of components (or Warps) is equal to the number of variables in the analysis, much of the variability in the sample is accounted for by the first several principal components (Johnson and Wichern, 2002). Principal components (or Warps) can then replace the initial variables without much loss of information on variation in the sample.

The principal components (PCs) are eigenvectors that describe major patterns of variation and represent a list of loadings of the original variables on the PC. The PCs are organised in a hierarchical order with the first one accounting for the most variation in the sample. The next component describes the maximum variance in the sample where variance described by the first PC is removed and so on. The PCs are orthogonal and uncorrelated with each other. The PC scores for each specimen describe the position of this specimen along the PC. Principal components for the inter-landmark data were calculated in the SPSS program (© SPSS Inc., 1989–2003).

The philosophy of Relative Warps stems from the method of fitting the thin-plate spline interpolation function into the coordinates of the landmarks for each specimen in a sample (Bookstein, 1989). The computation steps involve: i) extraction of the Partial Warps on the basis of the thin-plate spline function in a sample of aligned specimens using, for example, an average location of landmarks as reference; and ii) extraction of the principal components from the Partial Warp scores for each specimen (Bookstein, 1997; Rohlf, 1993). The results of the Partial Warps may be displayed, on one hand, in a classical way by the PC scores of each individual in the space of the principal components, thus allowing one to examine the morphological relationships between different individuals in the sample,

or each relative warp can be plotted as a deformation of the space of the reference configuration of the landmarks, visualising the aspects of variance in the sample described by the relative warp (Rohlf, 1993). The latter is achieved by computing a thin-plate spline for each relative warp.

For practical applications, it is noted that the results of Relative Warps are the same as the results of the extraction of principal components of the Procrustes residual coordinates (e.g. Slice, 2005; Gunz, 2005). Slice (2005) draws attention to one problem with the statistical usage of the Procrustes-processed data. The theory underlying many multivariate methods assumes a linear, Euclidian space. However, the geometry of the space (Kendall's space or the Procrustes hemisphere) is non-linear, thus violating the key assumption (Kendall, 1984; Slice, 2001). However, it has been shown by that an orthogonal projection from the Procrustes hemisphere to a linear space tangent at the sample mean best preserves the distances between the specimens and can be effectively used in the statistical analysis (Kent, 1994; Dryden and Mardia, 1998; Rohlf, 1999; Slice, 2001). Moreover, given the small variation found in most biological samples, using no projection does not violate the assumption of a linear space too badly. The formulae used in this work do not use the projection space for calculation of the Relative Warps.

Correlation analysis

Spearman and Kendall Rank correlations are used in the present work for establishing the linear association between age and shape of the frontal, as expressed by the Relative Warp scores for each individual, in order to verify ontogenetic trends in morphology. Correlation analysis evaluates the intensity of the association observed between two variables, without suggesting causal relationships between them (Sokal and Rohlf, 1995). The resulting

correlation coefficient may range from -1 for the absolute negative association to 1 for the absolute positive association. In the present work, the significance is tested with the aid of the two-tailed significance test that calculates the probability of obtaining results as extreme as the observed given the two-tailed normal distribution of the data. The calculation of the Pearson correlations has been performed in SPSS (© SPSS Inc., 1989–2003).

Discriminant analysis

Discriminant analysis is used here in order to solve group prediction for the unknown fossils on the basis of the first four Relative Warp scores for each individual. Discriminant analysis builds a predictive model of a group membership based on the observed characteristics of each case, for which group membership is known *a priori*, by means of generating new variables, the *discriminant function*. The discriminant functions represent linear combinations of the observed characteristics that provide the best discrimination between the groups. The classification problem is then solved by application of the discriminant functions to the values of the observed characteristics of the unknown specimens. The assignment of the individual to a group is made on the basis of the highest value of probability of the observed score given the membership of the individual in this group and given the associated degrees of freedom (*posterior probability*). The power of the discrimination is assessed by means of predicting group membership for individuals that are originally involved in the construction of the discriminant functions (see Johnson and Wichern, 2002).

The group membership prediction is connected with the size of the groups in the sample. If groups have approximately equal sizes, the prior probability of an unknown individual to belong to either one of these groups is equal. However, if group sizes differ dramatically,

the prior probability will depend on the size of the group. In the present work, the prior probabilities were assessed from the group sizes due to the considerably larger number of modern individuals compared to fossils. The accuracy of the original classification and the cross-validation classification are both reported. The latter is driven by an iterative procedure of leaving one individual out of an *apriori* assigned group and then its classification on the basis of the functions derived from the sample of all remaining individuals. The cross-validation of classification results provides for more realistic picture of the classification power than the original classification (Johnson and Wichern, 2002).

The assumptions for the discriminant analysis include independence of cases, multivariate normal distribution of the predictor variables, and homogeneity of within-group variance-covariance matrices across groups. The violation of the multivariate normality of distribution of the predictor variables creates no problem if discrimination between the groups is high. The homogeneity of the variance-covariance matrices may be assessed by inspection of scatter plots of scores on the first two discriminant functions produces separately for each group. Rough equality in overall size of the scatterplots is evidence of homogeneity of variance-covariance matrices. However, the inference from the Discriminant analysis is usually robust to heterogeneity of variance-covariance matrices if sample sizes are more-or-less equal and sufficiently large. Otherwise, cases tend to be overclassified into groups with greater dispersion (Johnson and Wichern, 2002; Tabachnik and Fidell, 2001). The discriminant analysis in this study is carried out using SPSS (© SPSS Inc., 1989–2003).

Multidimensional scaling

Multidimensional scaling is used here as an alternative method of displaying the information about similarities between individuals and/or group means in a low-dimensional space. This method is concerned with fitting the original data into a low-dimensional coordinate system such that any distortion caused by a reduction in dimensionality is minimised (Johnson and Wichern, 2002). The number of dimensions in the new coordinate system may take any value from 1 to $N-1$, where N is the number of individuals. Whereas the lowest possible number of dimensions for scaling might be preferred, the resulting match between the original data and its representation in the lower-dimensional space might not be perfect. The numerical measure of the closeness of match between the low-dimensional configuration and the original is *stress* (or Raw stress in STATISTICA package). The informal interpretation of the stress is as follows: 20% -- poor fit, 10% -- fair fit, 5% -- good fit, 2.5% -- excellent and 0% perfect fit. A second measure of discrepancy is *SS_{stress}* (or Stress in STATISTICA package) whose value is always between 0 and 1. Any value less than 0.1 is typically taken to mean a good representation of the objects by the points in the given configuration. As the number of scaling dimensions increases, the stress will decrease and become zero for $N-1$ dimensions (Johnson and Wichern, 2002).

In the present work, the original data are presented by Procrustes distances between individuals and/or group consensus shapes in the analysis, which may be taken as dissimilarity metrics. The multidimensional scaling does not hold any assumptions about the data distribution and the linearity of the relationship in the data. The multidimensional scaling is performed in STATISTICA (© StatSoft, Inc., 1995).

Group testing by permutation

The statistical inference for semi-landmark data has to be planned and performed with a certain amount of caution. For instance, there are far more semi-landmarks than specimens in detailed morphometric datasets (Gunz, 2005; see also Bookstein *et al.*, 1999, 2003).

Normally, the parametric statistical methods are not applicable in this case. Moreover, there is no actual statistical model of distribution available for semi-landmarks, which are not independent in their location (Gunz, 2005). Whereas the Relative Warp analysis is sufficient for the survey of the empirical datasets, the statistical inference requires a different approach that would not be tied up to any existing model. The Randomisation methods (see, for example, Good, 2000) are recommended for use in application to the semi-landmark data (Gunz, 2005).

In the present work, group differences were tested with the Monte-Carlo permutation procedure for which distances between mean shapes of the *two* tested groups (e.g. Moderns, Neanderthals or Upper Palaeolithic modern humans) were calculated and then groups re-shuffled. The groups were re-sampled 1000 times irrespective of the original identification of the individuals. The resulting *P*-value is reported as $(m+1)/(n+1)$, where *n* is the number of permutations generated and *m* is the number of permutations for which the distances between sampled groups equal or exceed the value actually observed. The calculations here are made in MATHEMATICA on the basis of formulae adapted from those developed by P. Mitteroecker and P. Gunz at the Institute for Anthropology, Vienna University.

All calculations related to generation and sliding semilandmarks, 3D reconstructions and Relative Warp analysis were performed in MATEMATICA.

Chapter 5 Results

Analysis of inter-landmark measurements

Reconstruction of inter-landmark distances

For the inter-landmark distances in a number of fossils, it was possible to achieve a certain amount of reconstruction by reflection (Tab.5.1). For this purpose, the 3D data for all landmarks and raw semilandmarks on the sagittal outline of each individual frontal bone were translated and rotated so that bregma took (0,0,0) coordinates, nasion took (x,0,0) coordinates and glabella took (x,y,0) coordinates. As a result, the sagittal outline was positioned in the surface of symmetry and symmetrical landmarks could be found by simple reflection of the coordinates of their existing counterparts.

Due to the bilateral asymmetry in human faces, it was expected that reconstruction by reflection might produce some inconsistencies with the original measurements (see (Mulick, 1965; Letzer and Kronman, 1967; Vig and Hewitt, 1975; Farkas and Cheung, 1981; Peck et al., 1991; Ferrario et al., 1993). To explore this question, a test was performed on five modern individuals for whom all original inter-landmark measurements were present.

The right set of symmetrical landmarks was re-calculated for each individual from their left counterparts. The new data were used for calculation of new inter-landmark distances. Euclidean distances were calculated within the sample of the five originals and their reconstructions for those 11 measurements. Distances were sorted into bins and frequencies plotted in Figure 5.1. It is easy to see that the distances between originals and

reconstructions (red) are smaller than inter-individual distances (blue). In order to expand the test, Euclidean distances between each of the tested originals and the rest of the recent individuals in the complete dataset (147 individuals) were calculated and compared with the distance to the respective original (Tab.5.2). Four individuals out of five had original–reconstruction distances smaller than the distances to any other individuals in the sample. One individual (Esk_20) had two inter-individual distances smaller than the original–reconstruction distance. This result is possibly representative of the reconstruction by reflection. It may be expected that original individual bilateral asymmetry introduces bias into the transverse diameters (making them, respectively smaller or larger in reconstruction), which may also affect measurements whose calculation is dependent on them, such as nasion-frontal angle (see Howells, 1973). However, the present test shows that the reconstruction by reflection works reasonably well for the majority of individuals and does not produce extensive error for the individuals where reflection resulted in biased transverse diameters.

Table 5.1 Fossils included in the analysis of inter-landmark measurements and reconstruction involved.

<i>Fossil name</i>	<i>Reconstructed landmarks</i>	<i>Measurements affected</i>
Abri Pataud	None	None
Amud	Sphenion right, Maxillofrontale right	Sphenion-sphenion, Interorbital breadth, Dacron subtense, Outer biorbital breadth
Broken Hill	None	None
Cro-Magnon 1	Dacron left	Interorbital breadth, Dacron subtense
Cro-Magnon 2	None	None
Cro-Magnon 3	Dacron right	Interorbital breadth, Dacron subtense
DV3	None	None

DV15	Dacron right	Interorbital breadth, Dacron subtense
DV16	None	None
Engis	Stephanion left, Frontotemporale left, Sphenion left, Frontomale anterior left, Frontomale orbitale left, Frontomale temporale left	Bistephanoid breadth, Sphenion-sphenion, Naso-frontal subtense, Naso-frontal angle, Bifrontal breadth, Outer biorbital breadth
Gibraltar1	Dacron right, Frontomale anterior left and right, Frontomale orbitale left and right, Frontomale temporale left and right	Interorbital breadth, Dacron subtense, Naso-frontal angle, Bifrontal breadth, Outer biorbital breadth
Kanalda	None	None
Khvalynsk	Frontomale anterior left, Frontomale orbitale left, Frontomale temporale left	Naso-frontal subtense, Naso-frontal angle, Bifrontal breadth
La Chapel aux Saints	None	None
La Ferrassie	Stephanion right, Sphenion right, Dacron right, Frontomale anterior right, Frontomale orbitale right, Frontomale temporale right, Maxillofrontal left	Sphenion-sphenion, Outer biorbital breadth, Bifrontal breadth, Naso-frontal angle, Interorbital breadth, Dacron subtense, Anterior interorbital breadth, Bistephanoid breadth
Le Moustier	Dacron right, Frontomale anterior right, Frontomale orbitale right, Frontomale temporale right, Maxillofrontale right	Naso-frontal subtense, Naso-frontal angle, Outer biorbital breadth, Bifrontal breadth, Interorbital breadth, Anterior interorbital breadth
Mladeč 1	Stephanion right, Frontotemporale right, Sphenion right, Dacron right	Bistephanoid breadth, Minimum frontal breadth, Sphenion-sphenion, Interorbital breadth, Dacron subtense
Mladeč 5	None	None
Neanderthal	Frontotemporale right	Minimum frontal breadth
Pavlov	Sphenion right	Sphenion-sphenion
Pech de l'Aze	Dacron left	Interorbital breadth, Dacron subtense
Podkumok	Dacron left	Interorbital breadth, Dacron subtense
Předmostí	Dacron right	Interorbital breadth, Dacron subtense
Qafzeh 1	Sphenion left	Sphenion-sphenion

Qafzeh 2	Sphenion right, Dacriion right	Sphenion-sphenion, Interorbital breadth, Dacriion subtense
Qafzeh 6	Sphenion right	Sphenion-sphenion
Šal'a	None	None
Satanay	None	None
Shanidar	Sphenion left, Dacriion right, Frontomolare anterior left, Maxillofrontale left	Sphenion-sphenion, Interorbital breadth, Dacriion subtense, Naso-frontal subtense, Naso-frontal angle, Outer biorbital breadth
Skhodnya	Dacriion right	Interorbital breadth, Dacriion subtense
Skhul V	Sphenion left, Dacriion left, Frontomolare anterior left, Frontomolare orbitale left, Frontomolare temporale left	Sphenion-sphenion, Interorbital breadth, Dacriion subtense, Naso-frontal subtense, Naso-frontal angle, Outer biorbital breadth
Starosel'e	None	None
Sungir' 2	None	None
Sungir' 3	None	None
Sungir' 1	None	None
Tabun	Stephanion left, Dacriion left, Frontomolare anterior left, Frontomolare orbitale left, Frontomolare temporale left, Maxillofrontale left	Bistephanoid breadth, Interorbital breadth, Dacriion subtense, Bifrontal breadth, Outer bifrontal breadth, Naso-frontal subtense, Naso-frontal angle
Teshik-Tash	None	None
Zuttiyeh	None	None

Table 5.2 Inter-landmark distances. Test of reconstruction: Euclidian distances between originals and reconstructions.

<i>Individual</i>	<i>Distance to the reconstruction</i>	<i>Number of distances that are smaller than the original--reconstruction</i>	<i>Proportion of distances smaller than the original--reconstruction</i>
Aus OC30980	2.86619	0	0
Brit Brand 859	18.776	0	0

Eg Af.11.5.467	7.41966	0	0
Esk 20 male	13.6586	2	0.0136054
KY 33 male	10.3621	0	0

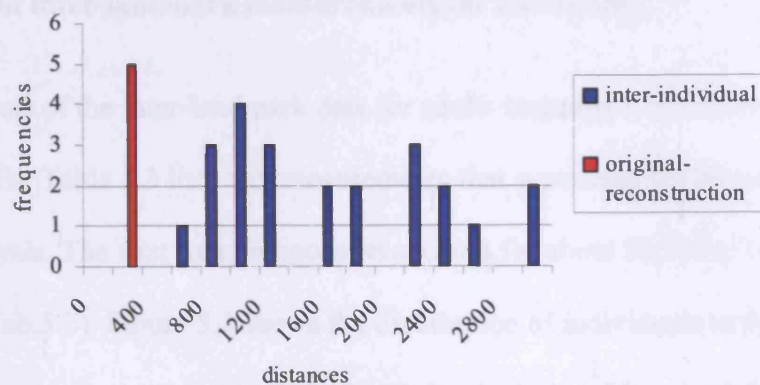


Figure 5.1. Inter-landmark measurements. Test of the reconstruction by reflection.

Analysis of inter-landmark measurements for adults only

The analysis of the inter-landmark data for adults included 142 individuals, 29 of which were fossils. Table 5.3 lists the measurements that were used for the principal component (PC) analysis. The first four components account for about 88.3% of the variation in the sample (Tab.5.3). Figure 5.2 shows the distribution of individuals in the space of the first two principal components. ‘Archaic’ hominins, including Neanderthals, the majority of the west Asian early modern humans and Broken Hill are separated from the modern individuals along PC2. Recent populations and the majority of the Upper Palaeolithic fossils demonstrate significant overlap on this graph. PC1 accounts for 44.4% of variation in the sample and has medium negative correlation with the size of the frontal, as described by the Frontal sagittal arc, Glabella bregma arc, Glabella bregma chord and Bifrontal breadth (Tab.5.2). Therefore, smaller individuals tend to locate at the positive pole of PC1.

The second principal component accounts for 22.7% of variation in the sample and is negatively correlated with Frontal angle from glabella, Outer biorbital breadth, Bifrontal breadth and Frontal angle (Tab.5.3). In other words, it separates flat frontals with relatively wide transverse diameters of the orbital region, found in the ‘archaic’ hominins, from the frontals with bulging forehead and relatively narrow orbital region as found in modern humans. The Russian fossils in the analysis, Skhodnya, Khvalysk, Sungir’ 1 and Podkumok are placed within the modern human distribution. However, Satanay is associated with Neanderthals along PC2 with Šal’a being the closest neighbour.

Table 5.3 Inter-Landmark distances. Adults. Component matrix and variance explained in the principal component analysis.

<i>Name of measurement</i>	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	<i>PC4</i>
Bifrontal breadth	-0.34732	-0.40843	-0.03876	0.159378
Frontal angle from glabella	-0.06872	-0.4242	-0.28012	-0.18414
Frontal angle	-0.03555	-0.40122	-0.2211	-0.26348
Frontal sagittal arc	-0.43848	0.34443	-0.16814	0.107065
Frontal sagittal chord	-0.3136	0.133058	-0.14049	-0.13237
Glabella-bregma arc	-0.43118	0.344427	-0.12756	0.0345
Glabella-bregma chord	-0.39059	0.114916	-0.17003	-0.13609
Bistephanoid breadth	-0.23325	0.000908	0.829437	-0.2902
Minimum frontal breadth	-0.27206	-0.22101	0.265141	-0.00998
Nasion-frontal angle	0.005476	-0.05461	0.13333	0.830903
Outer biorbital breadth	-0.34036	-0.41505	0.043758	0.218773
Eigenvalues	28404.8	14547.2	8183.9	5412.6
Variance explained	44.398%	22.738%	12.792	8.46%

Bold text highlights variables that have relatively high loadings onto respective component.

Recent populations greatly overlap in the space of the third and the fourth principal components (Fig.5.3) but demonstrate large differences in the span of variation between populations. Fossil individuals demonstrate very little association pattern, with the exception of a few Neanderthals at the negative end of PC4 (Fig.5.3). PC3 accounts for about 12.8% of the variation in the sample and is highly positively correlated with bistephanoid breadth. Tabun differs along this principal component due to the relatively large value of its bistephanoid breadth. PC4 accounts for about 8.5% of the variation in the sample and is highly positively correlated with Nasion-frontal angle. Five out of seven Neanderthals, Sal'a, Amud, Shanidar, La Chapelle aux Saints and La Ferrassie, cluster

together at the negative end of PC4 and are fairly close together along PC3 generally showing a high projection of the nasion and relatively average bistephanoid breadth. Neanderthal and Tabun do not confirm to this pattern showing great differences, comparable with ones within recent modern humans. Skhul V is markedly different from Neanderthals along PC4 due to its flat upper face. According to the present result, the upper face of Tabun is also somehow flatter than the face of the majority of Neanderthals.

Although there is little reason to doubt that Tabun and Skhul V indeed have flatter upper faces than European Neanderthals, one should be cautious in assessment of the degree of the difference because Nasion-frontal angle and Bistephanoid breadth are affected by reconstruction in Tabun and Nasion-frontal angle is affected by reconstruction in Skhul V. To the contrast with Skhul and Tabun, Khvalynsk, one of the Russian fossils in the analysis, is placed very low at the negative end of PC4 highlighting the high degree of the nasion projection (referred as the upper face projection hereafter). The reasoning applied to Skhul V and Tabun above should also be applied to Khvalynsk, where reconstruction affects the Nasion-frontal angle and may bias the measurement towards the narrower upper face and respectively narrower Nasion-frontal angle. However, given the results of the reconstruction test above, I expect that the general trends in Skhul V, Tabun and Khvalynsk are correct even though the degree of deviation may be overestimated due to the reconstruction bias.

Skhodnya is very similar to Broken Hill in the space of PC3 and PC4 being just at the edge of the recent human distribution. This result points to a relatively narrow posterior aspect of these two frontals coupled with a slightly more projecting upper face. Sungir' 1, Satanay and Podkumok fall within the range of variation of recent modern populations together with

the majority of the Upper Palaeolithic individuals in the comparative sample. Unlike in the space of the first two components, here Satanay is more similar to such forms as Pavlov and DV16 due to the narrow posterior aspect of the frontal and an average projection of the upper face.

In sum, this analysis first of all shows clear differentiation between modern and archaic hominins in the comparative sample. At the same time, the majority of the Neanderthals overlap with West Asian and African fossils. Recent and Upper Palaeolithic modern humans mostly overlap in the space of the first four PCs. Sungir' 1 and Podkumok fall well within this modern pool of variation. Khvalynsk and Skhodnya, although associated with modern humans by the majority of features, also show some differences. Skhodnya is marginally different from modern humans and close to Broken Hill in the combination of the narrow posterior aspect of the frontal and more projected upper face. Khvalynsk may possibly be similar to Neanderthals in the high projection of the upper face, but this result needs further investigation. Out of all the Russian fossils, Satanay is the most similar to the generalised 'archaic' group of hominins but does not associate with Neanderthals in particular features of morphology.

An attempt at classification is made with the help of Discriminant analysis of a three *a-priori* groups that have prior probabilities assigned in accordance with the group sizes (Tab.5.4). A step-wise Discriminant analysis has been run on the first 11 PCs using Wilks' Lambda as a parameter for choice of principal components that have the most discriminating power. Six chosen principal components (Tab.5.5) account for about 79.87% of variation in the sample. Two significant discriminant functions were received that provide for 95.4% of the correct classification in the original analysis and 93.9% of the

correct classification during the cross-validation. The structure matrix is given in the Table 5.5 and the scatter of individuals in the space of the two discriminant functions in Figure 5.4. However, on close inspection of the classification results, it is revealed that the Upper Palaeolithic group is not very stable: four out of 11 individuals are assigned to the recent modern human group in the original analysis and five during cross-validation (Tab.5.6). Two of the Neanderthals (Tabun and Neanderthal) were also classified as recent modern humans (Tab.5.7).

Table 5.4 Inter-Landmark distances. Adults. *A-priori* groups and ungrouped individuals in the Discriminant analysis.

<i>Group</i>	<i>Composition</i>	<i>Number of individuals</i>
Recent modern humans	9 populations	113 individuals
Upper Palaeolithic	Abri Pataud, Cro-Magnon 1, Cro-Magnon 2, Cro-Magnon 3, DV3, DV15, DV16, Mladeč 1, Mladeč 5, Pavlov, Předmostí 3	11 individuals
Neanderthal	La Chapell aux Saints, La Ferrassie, Neanderthal, Šal'a, Tabun, Amud, Shanidar	7 individuals
Ungrouped	Broken Hill, Kanalda, Khvalynsk, Podkumok, Satanay, Skhodnya, Sungir1, Skhul V, Qafzeh1, Qafzeh2, Qafzeh6, Zuttiyeh	11 individuals

Table 5.5 Inter-Landmark distances. Adults. Structure matrix for the discriminant analysis of 6 PCs.

<i>Variable</i>	<i>Function 1</i>	<i>Function 2</i>
PC 1	.429(*)	-0.015
PC 2	0.359	.837(*)
PC 6	-0.247	.371(*)

PC 7	.229(*)	-0.144
PC 8	-.339(*)	0.112
PC 9	.398(*)	-0.265

(*) Marks largest absolute correlations between discriminant functions and respective Principal Components.

Table 5.6 Inter-Landmark distances. Adults. Summary of classification results in the original analysis and after cross-validation.

	<i>Original group membership</i>	<i>1</i>	<i>2</i>	<i>3</i>
<i>Predicted group membership during classification</i>				
<i>Original analysis</i>	1	112 (99.1%)	0	1(0.9%)
	2	4 (36.4%)*	7 (63.6%)	0
	3	1 (14.3%)*	0	6 (85.7%)
<i>Cross-validation</i>	1	112 (99.1%)	0	1(0.9%)*
	2	5 (45.5%)*	6 (54.5%)	0
	3	2 (28.6%)*	0	5 (71.4%)

(*) Bold text marks numbers and rate of erroneous classifications.

Table 5.7 Inter-Landmark distances. Adults. Classification results for ungrouped individuals.

	<i>First predicted group</i>	<i>Squared Mahalanobis distance to centroid*</i>
<i>Maximum distance within the recent modern group to its centre</i>		10.23
<i>Maximum distance in the Upper Palaeolithic group to its centre</i>		8.27
<i>Maximum distance within the Neanderthal group to its centre</i>		4.77

<i>Broken Hill</i>	NEA	3.976
<i>Qafzeh 1</i>	MOD	2.589
<i>Qafzeh 2</i>	MOD	7.035
<i>Qafzeh 6</i>	NEA	0.309
<i>Skhul V</i>	NEA	1.085
<i>Zuttiyeh</i>	NEA	0.596
<i>Khvalynsk</i>	MOD	0.024
<i>Podkumok</i>	MOD	0.202
<i>Satanay</i>	MOD	4.965
<i>Skhodnya</i>	MOD	0.631
<i>Sungir 1</i>	MOD	2.79

To the opposite of expectations, Qafzeh 6 and Skhul V do not associate with modern humans but are classified as Neanderthals. The older west Asian fossil from Zuttiyeh is also found to be close to Neanderthals. In addition, it is interesting to note that Broken-Hill has also been classified as a Neanderthal but it falls outside the 95% distribution of the Neanderthal sample (Fig.5.4).

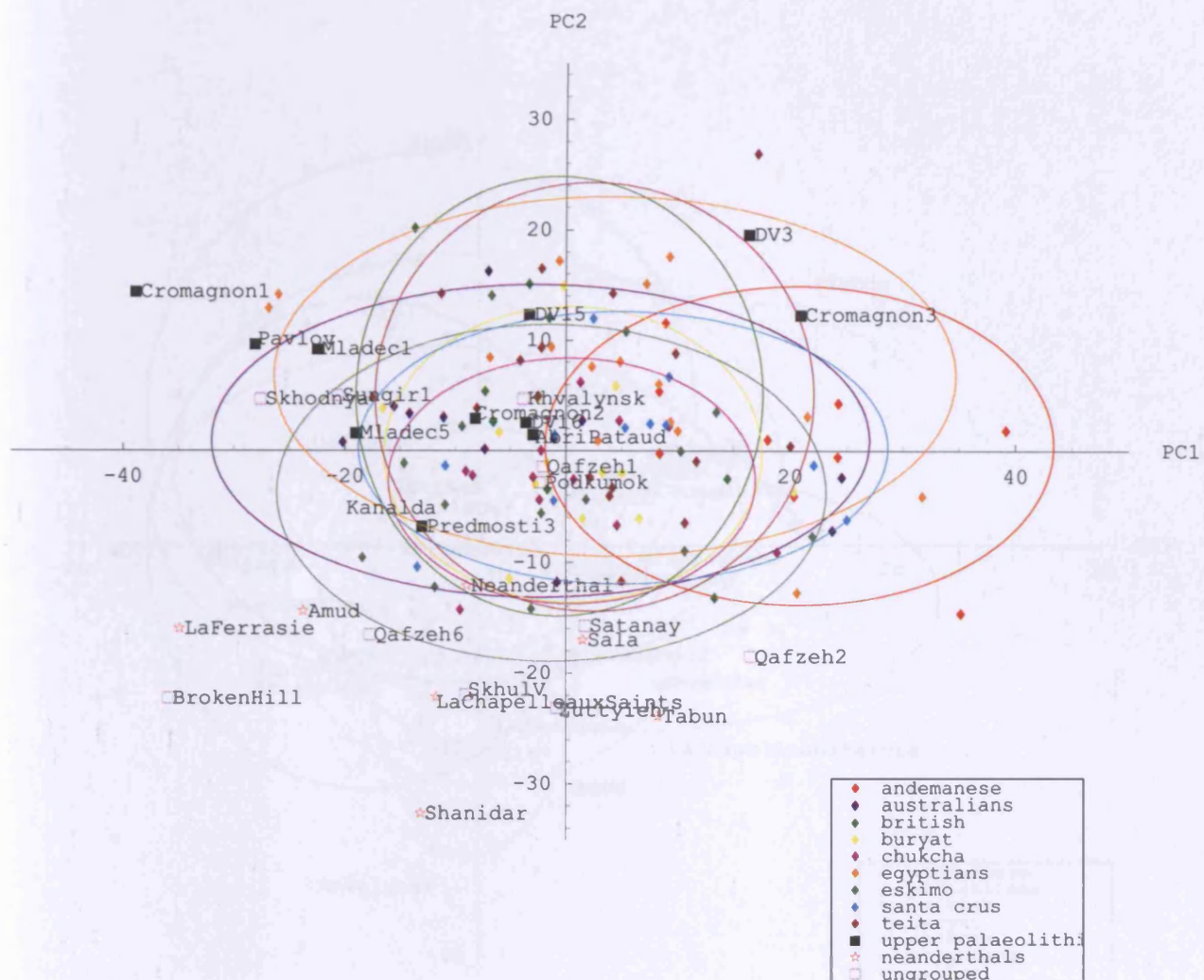


Figure 5.2. Inter-landmark measurements. Adults. Distribution of individuals in the space of the first and second principal components.

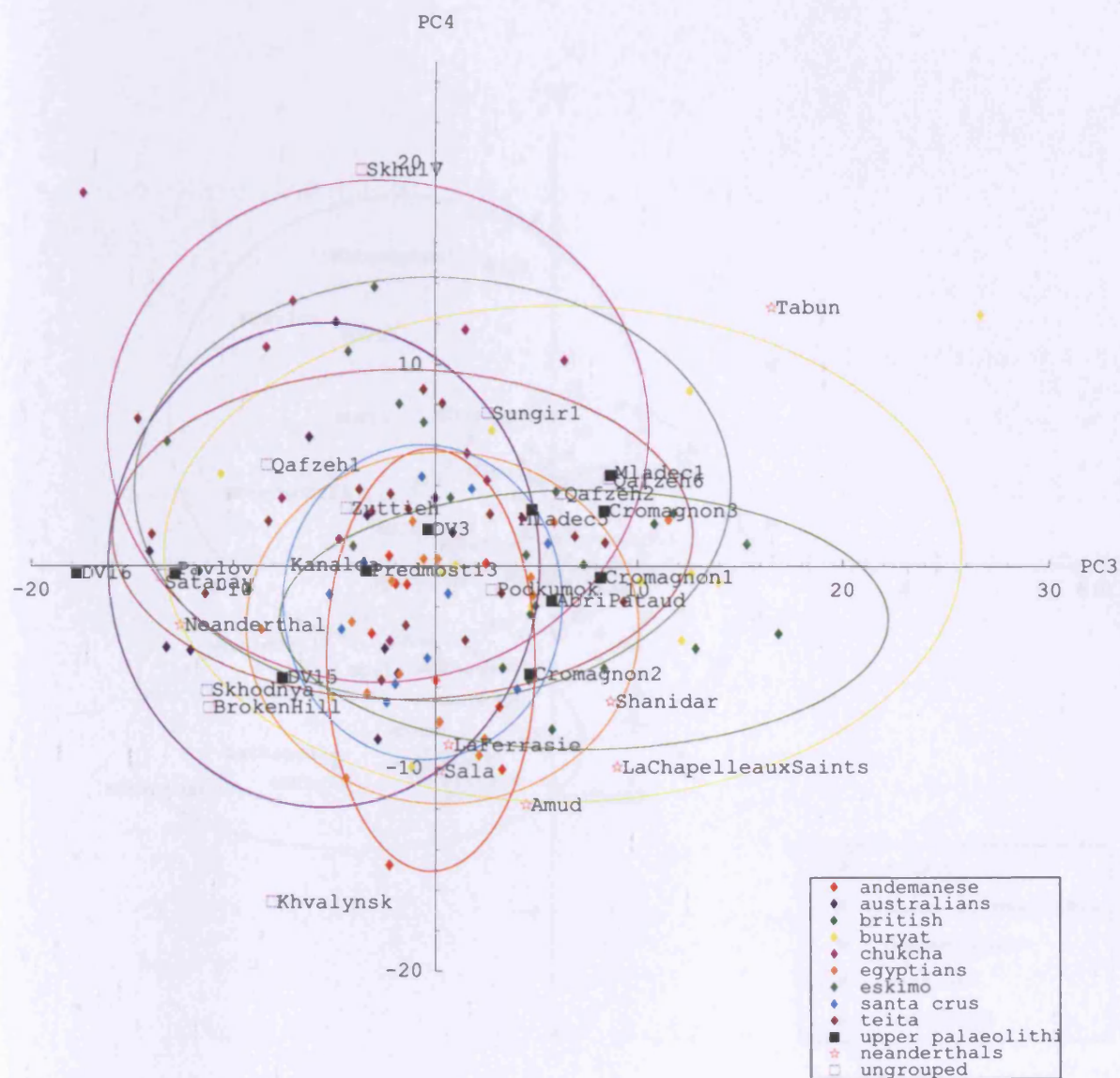


Figure 5.3. Inter-landmark measurements. Adults. Distribution of individuals in the space of the third and fourth principal components.

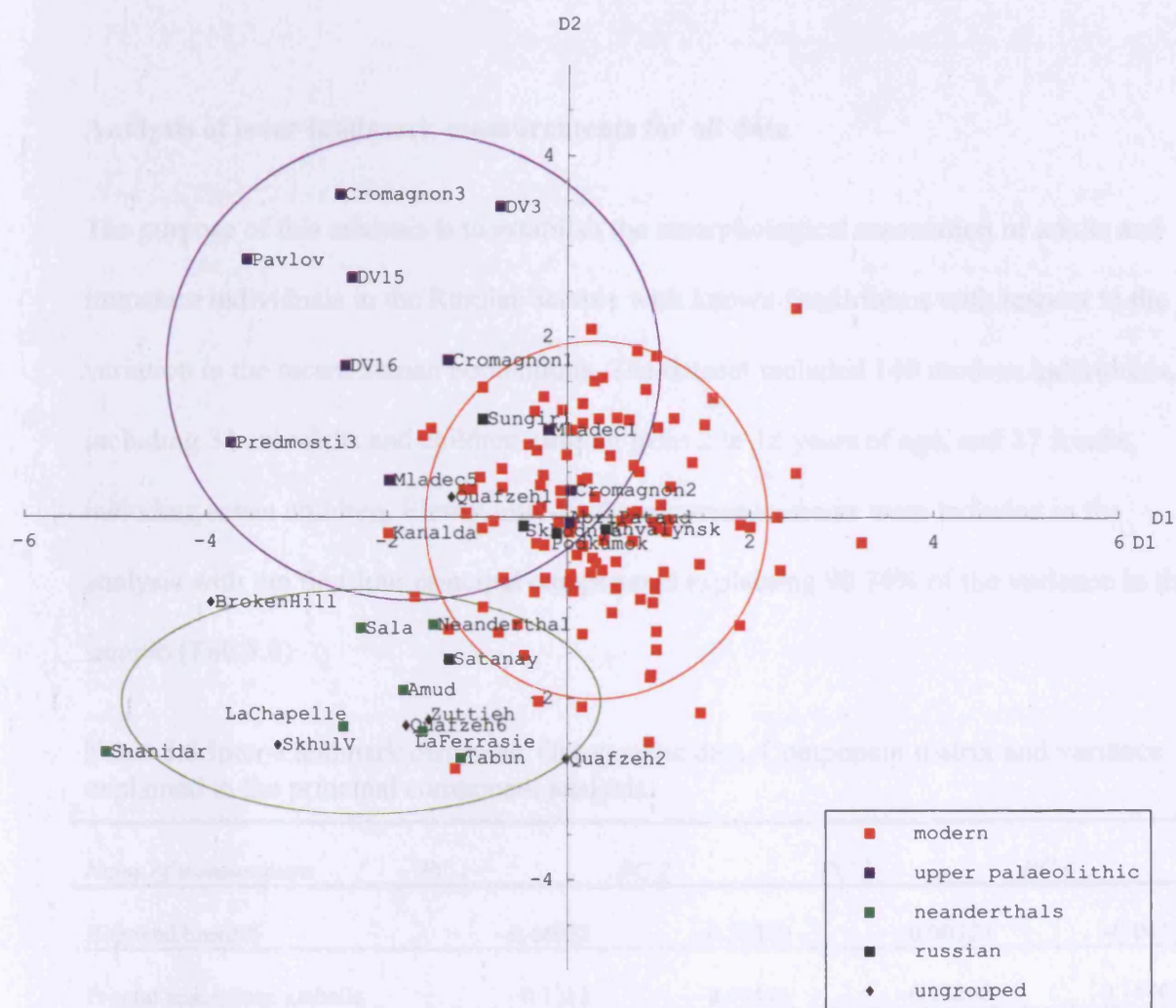


Figure 5.4. Inter-landmark measurements. Adults. Discriminant analysis: three a-priori groups, 6 principal components describing 96.6% of variation in the sample.

Analysis of inter-landmark measurements for all data

The purpose of this analysis is to establish the smorphological association of adults and immature individuals in the Russian sample with known fossil forms with respect to the variation in the recent human populations. The dataset included 149 modern individuals, including 34 subadults and children ranging from 2 to 18 years of age, and 37 fossils, including seven children. Eleven inter-landmark measurements were included in the analysis with the first four principal components explaining 90.74% of the variance in the sample (Tab.5.8)

Table 5.8 Inter-Landmark distances. Ontogenetic data. Component matrix and variance explained in the principal component analysis

<i>Name of measurement</i>	<i>PC 1</i>	<i>PC 2</i>	<i>PC 3</i>	<i>PC 4</i>
Bifrontal breadth	-0.44022	-0.32269	-0.00328	-0.04171
Frontal angle from glabella	-0.1313	-0.40121	-0.28393	0.144008
Frontal angle	-0.12602	-0.40156	-0.23264	0.200777
Frontal sagittal arc	-0.34006	0.42112	-0.15273	-0.06641
Frontal sagittal chord	-0.29714	0.173169	-0.14976	0.067588
Glabella-bregma arc	-0.35532	0.436276	-0.14042	0.032834
Glabella-bregma chord	-0.35966	0.19748	-0.19312	0.127847
Bistephanoid breadth	-0.20596	0.05946	0.804446	0.157164
Minimum frontal breadth	-0.2501	-0.12026	0.329089	0.125858
Nasion-frontal angle	-0.10655	-0.07828	0.047371	-0.9271
Outer biorbital breadth	-0.4441	-0.33595	0.069328	-0.10373
Eigenvalues	57379.9	19577.1	9921.1	7417.5

Variance explained	55.332%	18.817%	9.544	7.059%
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The distribution of individuals of the first four PCs is shown in Figure 5.5. The first PC has medium negative correlation with Bifrontal breadth, Outer biorbital breadth, Glabella-bregma arc, Frontal sagittal chord and Frontal sagittal arc describing the size of the frontal (Tab.5.8) and significant negative correlation with age (Tab.5.9). Therefore, smaller and younger individuals, such as Pech de l'Aze, Starosel'e and Engis are located at the positive end of PC 1 (Fig 5.5a).

Table 5.9 Inter-Landmark distances. Ontogenetic data. Correlation of the principal components with age.

	<i>Spearman Rank correlation</i>	<i>t-test of significance at 0.01% level</i>	<i>Kendal Rank correlation</i>	<i>t-test of significance at 0.01% level</i>
PC1	-0.57	True	-0.46	True
PC2	-0.22	False	-0.17	False
PC3	-0.11	False	-0.09	False
PC4	-0.13	False	-0.1	False

The second PC separates 'archaic' hominins from the majority of the modern humans (Fig.5.5b). As in the previous analysis, 'archaic' encompasses Neanderthals, west Asian hominins and Broken Hill, whereas 'modern' include both recent and Upper Palaeolithic individuals. PC 2 is positively correlated with Glabella-bregma arc, Frontal sagittal arc, and negatively with Frontal angle and Frontal angle from glabella. It also shows negative correlation with Bifrontal breadth and Outer bifrontal breadth thus separating forms with

relatively bulging foreheads and narrow orbital region, as in modern humans, from flat frontals with expanded supraorbital region, as in 'archaic' individuals.

PC 3 accounts for 9.5% of variation in the sample and is highly positively correlated with Bistephanoid breadth. There is very little pattern apparent along this component Fig 4.5c.

PC 4 accounts for about 7% of variation in the sample and has very high loading on the Nasion-frontal angle. Neanderthals, apart from Tabun tend to occupy the positive end of PC 4 (Fig.5.5d), which highlights the high projection of their upper face. However, Neanderthal, Le Moustier and Shanidar overlap with modern human distribution in this feature. Engis appears to have the most projecting face, which, however, could have been enhanced in Engis by the reconstruction bias (Tab.5.1). Teshik-Tash falls closer to modern humans rather than Neanderthals along PC4. In other words, it differs from Neanderthals in the lower projection of its upper face.

Ponce De León and Zollikofer (2001) demonstrated that modern humans and Neanderthals have different ontogenetic trajectories in their 3D analysis of the cranial morphology. They believe that the differences are caused by early, prenatal, divergence in morphology with postnatal parallelism of developmental patterns. It was therefore expected that a similar picture could be obtained on the inter-landmark data and tested Russian fossils would associate with the forms of the appropriate age and taxonomic status. However, ontogenetic trends in the present analysis are not very well seen in the two-dimensional representation. Figure 5.5 shows that Neanderthals differentiate from modern groups (both, recent and Upper Palaeolithic) along the second and the fourth PC. Figure 5.6 plots these two PCs together with the PC1, which is correlated with age. As a result, one can observe that the majority of Neanderthals, including children, are positioned above the cloud formed by the

recent and Upper Palaeolithic modern individuals. Within this picture, it is notable that Starosel'e takes position among young modern individuals, whereas Teshik-Tash borders modern humans' distribution and Neanderthal trend. However, in this projection Teshik-Tash is located closer to the modern humans due to the influence of the PC4, whereas it falls within the 50% distribution of adult Neanderthals in both, PC1 and PC2 (Fig.5.5 a and b). The other two Neanderthal infants in the analysis, Pech de l'Aze and Engis are under 4 years of age and fall well outside of the distribution of adult Neanderthal along the PC1 (Fig 5.5a). This phenomenon can be explained by the fact that adult neurocranial size in modern humans is 90% achieved by the age of six (Humphrey, 1998) and Neanderthals could have had even faster growth (Rozzi and de Castro, 2004) so that by the age of nine, Teshik-Tash is already close in size to adult forms. The shape of the Teshik-Tash frontal as described by PC 2 is similar to 'archaic' forms, including Neanderthals.

The Upper Palaeolithic children Sungir' 2 and 3 of about 13 and 9 years of age, respectively, are placed within the adult modern human distribution. The Satanay frontal takes position among adult individuals of all groups along PC1. Therefore, it most likely belongs to an adult individual. Among unexpected results highlighted by the 3D figure (Fig 5.6), is association of Khvalynsk with the Neanderthals, which mostly due to the influence of the PC4, i.e. the high projection of the upper face in Khvalynsk.

In total, separate ontogenetic trends of Neanderthals and modern humans can be observed on the inter-landmark distance data if several components are taken into account. The present analysis established the association of Teshik-Tash with adult 'archaic' forms and to a lesser extent with Neanderthals in the upper face projection as described by PC 4 in the analysis. The summary of information from the first four principal components indicates

that Starosel'e is possibly most closely associated with modern humans, as opposed to the Neanderthal infants of similar age from Engis and Pech de l'Aze who cluster together with Neanderthals along PC 4. Sungir' 2 and 3 are firmly placed within the modern human variation.

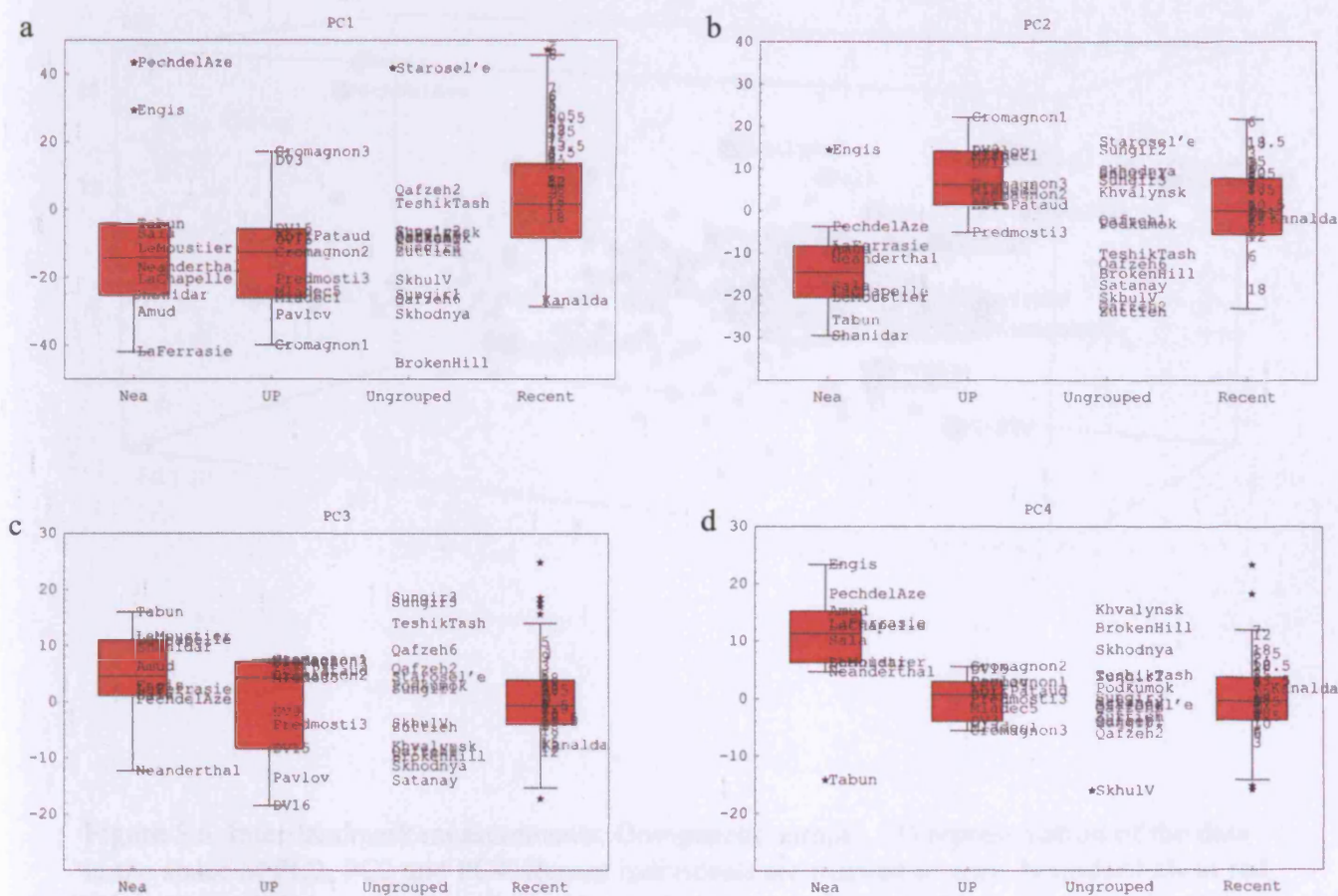


Figure 5.5. Inter-landmark measurements. Ontogenetic sample. One-dimensional Box-plot representation of the first four PCs. The red box contains the middle 50% of the data between the 75th (top) and the 25th (bottom) percentile of the data. The horizontal line in the box denotes median, whiskers indicate minimum and maximum of 1.5 times the inter-quartile range. Individually plotted observations (*) are outliers.

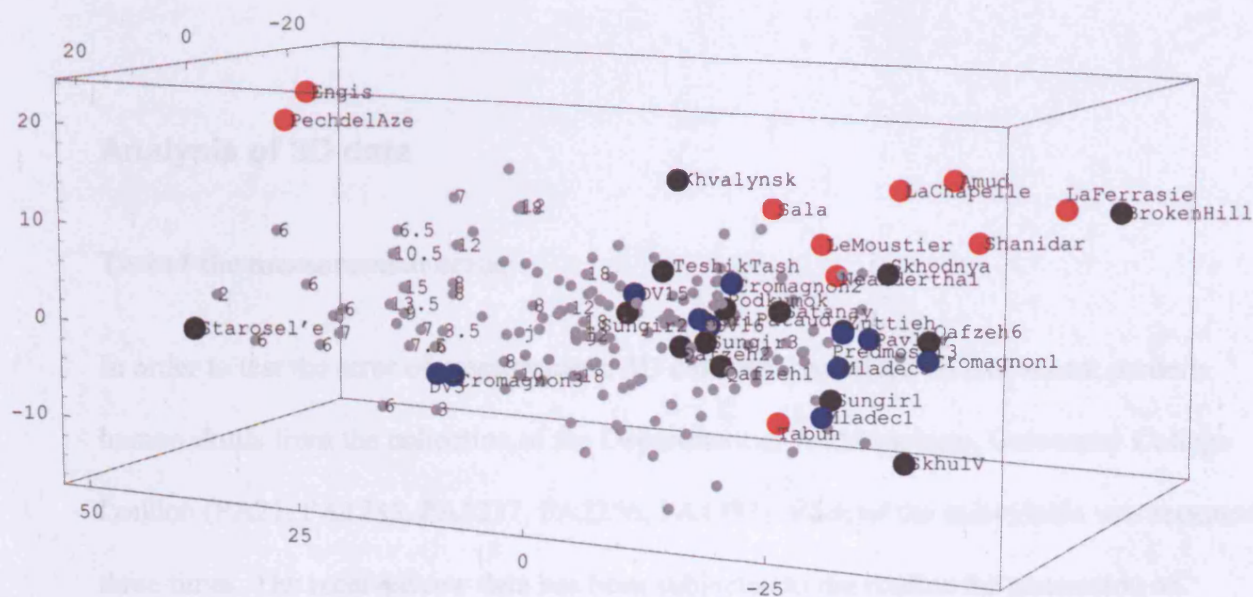


Figure 5.6. Inter-landmark measurements. Ontogenetic sample. 3D representation of the data in the space of PC2, PC2 and PC4. Recent individuals are marked in gray, Neanderthals in red, Upper Palaeolithic modern humans in blue and ungrouped fossils in black. Recent sub-adults are additionally marked by their age.

Analysis of 3D data

Test of the measurement error

In order to test the error of measurement, 3D data were collected on five recent modern human skulls from the collection of the Department of Anthropology, University College London (PA21, PA1235, PA1237, PA1256, PA1491). Each of the individuals was repeated three times. The received raw data has been subjected to the routine for generation of semilandmarks on the outlines and surfaces as described in the Methods section. Procrustes distances have been then calculated between repeats of each individual and mean, median, minimum and maximum distances have been found and interpreted as metrics for the measurement error (Tab.5.10).

Table 5.10 3D data. Test of the measurement error.

<i>Mean distance between repeats (mean error)</i>	<i>Median distance between repeats (median error)</i>	<i>Minimum distance between repeats (minimum error)</i>	<i>Maximum distance between repeats (maximum error)</i>
0.001757	0.001869	0.001046	0.002602

In the next step, inter-individual Procrustes distances have been calculated (i.e. distances between each of the repeats of every individual and all other individuals in the sample). A test has been run in order to find any intra-individual distances that would be larger or equal inter-individual distances in the sample. No such distances have been found. Therefore, it is concluded that the measurement error does not affect the result.

Reconstruction test

The TPS reconstruction is chosen as the best suited reconstruction method for the type of data to be reconstructed and the following use of it in the statistical analysis (see Methods section). The application of the TPS reconstruction to the frontal bone has been tested on five complete modern individuals. For this purpose, some of the 3D points were deleted from the raw dataset (Figure 5.7) and then reconstructed following the protocol described in the Methods section. Then, Procrustes distances were calculated between individuals in the sample of five originals and their respective reconstructions. Figure 5.8 plots distances sorted into bins. Distances between originals and reconstructions are shown in red and inter-individual distances are shown in blue. In sum, original–reconstruction distances are consistently smaller than inter-individual distances in this sample.

Further analysis involved calculation of Procrustes distances between each of the tested originals and all other individuals in the 3D sample of recent populations (122 individuals) and then comparing them with the distances between the respective original and its reconstruction. Table 5.11 presents the results of the test.

Table 5.11 3D data. Reconstruction test: distances between originals and reconstructions.

<i>Individual</i>	<i>Distance to the reconstruction</i>	<i>Number of distances that are smaller than the original–reconstruction</i>	<i>Proportion of distances smaller than the original–reconstruction</i>
Aus_Cam2123	0.00302	0	0
Brit_Brand_765_juv	0.00139	0	0
Bur_4610	0.00099	0	0
Eg_E6	0.00321	3	0.02459
Esk_7	0.00021	0	0

Four out of five individuals have shortest distances to their respective reconstructions. One individual, Eg_E6, has three out of 122 inter-individual distances shorter than the distance between the original and reconstruction. Referring to Figure 5.7, one can see that this individual had large parts of its temporal regions reconstructed, including zygomatic processes. The poorer performance of the TPS function in this case is expected because zygomatic processes break the otherwise smooth shape of the frontal bone (Gunz, 2005). However, the comparison with inter-individual distances here involves comparison within fairly homogenous populations, thus increasing chances of finding similar individuals, and the proportion of inter-individual distances that are smaller than the original–reconstruction distance is very low (about 2.5%). Also, the mean distance to the reconstruction is comparable to the mean measurement error (Tab.5.10). I suggest two points that may justify use of the TPS function for further application:

1. Only those fossils that have relatively small areas absent will be subjected to TPS reconstruction; other means of reconstruction, such as reflection, will be applied if there are large areas of the frontal missing and the original fossil is not visibly distorted, providing for a smooth final result;
2. In the absence of the original reference points that bend TPS in their vicinity and if the absent areas are not smooth but represent processes, notches or have other complicated topography, the function tends to substitute reference shape for the absent parts of the template (see Methods). Therefore, one can expect that differences between the reconstructed fossil and the reference shape in the zygomatic processes of the frontal will not be as pronounced as would be otherwise if the fossil was intact. In other words, the reconstruction with the help of the TPS

function will diminish rather than magnify differences. As a result, the observed differences in the comparative sample of fossils and recent individuals may be taken as a conservative estimation of the real differences.

Given that reconstruction with the help of TPS function requires usage of a template, it was important to find out how choice of the template affects the result. Gunz (2005) reports reconstruction of several specimens of *Australopithecus africanus* with the help of two different reference shapes. Human and chimp infants were used for reconstruction of the Taung child. Sts 5 and MLD 37/38 were used as references for the reconstruction of Sts 71. Sts 5 and Sts 71 were used for reconstruction of Stw 505. In the cases of Taung child and Sts 71, the different reconstructions gained very similar results. However, in the case of Stw 505, two resulting reconstructions were noticeably different "...reflecting the shape difference between the reference crania" (Gunz, 2005, p.123).

In order to test the issue of the reconstruction reference in the present work, five modern individuals that have been used for the reconstruction test above were subjected to five further reconstructions on the basis of a number of individuals of different age and taxonomic status: a British juvenile (Brit_Brand_juven_868), an adult male Buryat (Bur_4587), Broken-Hill, Cro-Magnon 1 and La-Chapelle-aux-Saints. In his choice of references, Gunz (2005) uses criteria of potential similarity in the shape between the reconstruction and the reference that are reflected in the close phylogenetic relationships and age of individuals. Here, I intentionally incorporate references of different age and phylogenetic status for reconstruction of modern individuals in order to predict how the reconstruction of the fossil hominins on the basis of the modern human consensus shape may affect the result

Final sample of individuals for the test included 35 shapes consisting of original modern human frontals, their first reconstruction by the adult or the child consensus shape, as was appropriate for the age of the original, and five additional reconstructions of each individual. Procrustes distances were calculated between the original and all reconstructions of one individual and compared with the distances between individuals (originals and reconstructions). The number of inter-individual distances smaller than distances within individuals was taken as a measurement of the inconsistency of reconstructions. Table 5.12 provides for the results of this test.

Table 5.12 3D data. Reconstruction test: test of TPS reconstruction by different reference shapes.

<i>Name of the original</i>	<i>Number of intra-individual distances larger than inter-individual distances (total 49)</i>	<i>Percent</i>	<i>Number of inter-individual distances smaller than intra-individual distances (total 196)</i>	<i>Percent</i>
Aus_Cam2123	1	2.04%	2	1.02%
Brit_Brand_765_juv	2	4.08%	4	2.04%
Bur_4610	none	0	none	0
Eg_E6	6	12.24%	38	19.4%
Esk_7	none	0	none	0

Reconstructions for two out of five individuals yielded consistent results irrespective of the reference shape. Expectably, these two individuals, Bur_4610 and Esk_7 have the smallest areas reconstructed (Fig.5.7). The reconstructed areas in the remaining three individuals are larger with Eg_6 being the most affected. This result offers an immediate conclusion that

the choice of the reference shape is more important when missing areas are large. In the case of Brit_Brand_765_juv and Eg_6 missing areas encompass zygomatic processes hence making the reconstruction even more imprecise (see above).

Considering each reconstruction, the worst performance in the case of the Australian individual (Aus_Cam2123) was given by the reconstruction with the help of Brit_Brand_juven_868 reference. For the Brit_Brand_765_juv individual, the worst reconstruction was by Broken Hill. In the case of Eg_E6 reconstructions by the juvenile individual (Brit_Brand_juven_868) and by the male Buryat (Bur_4587) were the worst even in comparison with the reconstructions by Broken-Hill and La-Chapelle-aux-Saints. In this case, the poor reconstruction performance was clearly called upon by differences in the shape of the temporal regions between the original adult Egyptian and juvenile, on one hand, and 'mongoloid', on the other, shapes of the references. Therefore, the present result supports the suggestion by Gunz (2005) to choose such reconstruction reference shapes, which are not expected to have large deviation from the final shape of the original. In this respect it is surprising that the reconstructions by the fossil reference shapes, quite different from the recent modern human original (Broken-Hill and La-Chapelle-aux-Saints), have performed well in the general picture of the reconstruction test. This phenomenon may only be explained by the fact that the reconstructed areas did not include features that are especially distinctive for these fossil forms. In all cases, reconstructions by the age-appropriate consensus shape have performed best for all individuals. It is decided to carry out reconstructions of the incomplete fossils in the analysis using these reference shapes.

Table 5.13 shows the list of fossils that were subjected to the reconstruction. The adult consensus shape for the recent individuals has been used as a reference for adult fossils and

a juvenile consensus shape for recent modern humans was used for reconstruction of missing parts in fossil children.

Table 5.13 3D data. Fossils included in the analysis and reconstruction involved.

<i>Name of the fossil</i>	<i>Reconstructed landmarks</i>	<i>Reconstructed areas</i>
Abri Pataud	None	None
Amud	Sphenion right, Dacriion left and right, Maxillofrontale right	Medial portions of both orbital rims and distal end of the right temporal area
Broken Hill	None	None
Cro-Magnon 1	Dacriion left	Small area on the inside of the left medial orbital plate
Cro-Magnon 2	None	None
Cro-Magnon 3	Dacriion right	Small area on the inside of the right medial orbital plate
DV1	Frontotemporale left, Dacriion left and right, Frontomalare anterior left and right, Frontomalare orbitale left and right, Frontomalare temporale left and right	Small distal part of the left temporal area, left zygomatic process, small lateral portion of the right, medial portions of the left and right orbits
DV3	None	None
DV15	Dacriion right	Small area on the inside of the right medial orbital plate
DV16	None	None
Engis	Stephanion left, Frontotemporale left, Sphenion left, Frontomalare anterior left, Frontomalare orbitale left, Frontomalare temporale left	A large area of the left part of the frontal is absent; the reconstruction was performed by means of reflection of the right part
Gibraltar 1	Bregma, Stephanion left, Frontotemporale left, Sphenion left, Frontomalare anterior left, Frontomalare orbitale left, Frontomalare temporale left	About quarter of the posterior surface of the frontal squama on the left side spanning over bregma; small distal end of the left zygomatic process. Reconstructed by reflection.

Gibraltar 2	Dacrion right, Frontomale anterior left and right, Frontomale orbitale left and right, Frontomale temporale left and right	Small area on the inside of the right medial orbital plate; distal ends of both zygomatic processes
Kanalda	None	None
Khvalynsk	Frontomale anterior left, Frontomale orbitale left, Frontomale temporale left	Small distal parts of the temporal areas; nasion and medial portions of the orbits
La Chapell aux Saints	None	Small area at the posterior portion of the frontal squama on the left
La Ferrassie	Stephanion right, Sphenion right, Dacrion right, Frontomale anterior right, Frontomale orbitale right, Frontomale temporale right, Maxillofrontale left	Posterior portion of the frontal squama on the right; small distal part of the left temporal region; distal part of the right zygomatic process
La Quina	Nasion, Sphenion left, Dacrion left and right, Maxillofrontale left and right	Nasal area; left temporal area
Le Moustier	Dacrion right, Frontomale anterior right, Frontomale orbitale right, Frontomale temporale right, Maxillofrontale right	Distal part of the right zygomatic process; inside of the right medial orbital plate spanning over to the nasal area but not to nasion
Mladeč 1	Stephanion right, Frontotemporale right, Sphenion right, Dacrion right	Left temporal area including about 2/3 of the left temporal line (both zygomatic processes, however, are mostly intact)
Mladeč 2	Sphenion left and right, Dacrion left and right, Frontomale anterior left and right, Frontomale orbitale left and right, Frontomale temporale left and right	Both distal temporal areas; distal portions of both zygomatic processes, including distal ends of the lateral orbital portions
Mladeč 5	Dacrion left and right, Frontomale orbitale left and right	Small areas on the inside of both medial orbital plates; distal ends of the lateral portions of the orbital rims on both sides
Neanderthal	Frontotemporale right	Small area around Frontotemporale right
Pavlov	Dacrion left and right, Sphenion right	Small areas on the inside of the both medial orbital plates, distal portion of the right temporal area
Pech de l'Aze	Dacrion left	Small area on the inside of the left medial orbital plate
Podkumok	Sphenion left and right, Dacrion left, Maxillofrontale left	Distal parts of the temporal areas; medial part of the left orbit

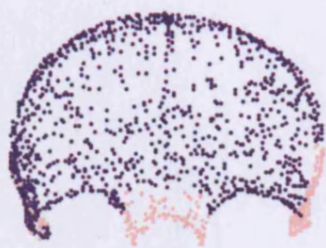
Předmostí 3	Dacryon right, Maxillofrontale left and right	Distal temporal region on the left; lateral areas of the nasal region on both sides
Qafzeh 1	Sphenion left	Distal left temporal area
Qafzeh 2	Sphenion right, Dacryon right	Distal left temporal area and the inside portion of the medial orbital plate on the right
Qafzeh 6	Sphenion right	Distal right temporal area and the inside portion of the medial orbital plates on both sides
Šal'a	None	None
Satanay	None	None
Shanidar	Sphenion left, Dacryon right, Frontomale anterior left, Maxillofrontale left	Left temporal region and medial portion of the left orbit
Singa	Frontomale anterior left and right, Frontomale orbitale right, Frontomale temporale left and right	Central and lateral portions of the right orbit; distal part of the right zygomatic process; small anterior and posterior aspects of the distal part of the left zygomatic process
Skhodnya	Sphenion left and right, Dacryon right, Maxillofrontale right	Medial portion of the right orbit; distal parts of both temporal areas
Skhul V	Sphenion left, Dacryon left, Frontomale anterior left, Frontomale orbitale left, Frontomale temporale left	Medial portion of the left orbit; Glabella, distal end of the left zygomatic process and distal part of the left temporal area
Starosel'e	Dacryon left and right	Inside of the left and right medial orbital plates
Sungir' 1	None	None
Sungir' 2	None	None
Sungir' 3	None	None
Tabun	Stephanion left, Dacryon left, Frontomale anterior left, Frontomale orbitale left, Frontomale temporale left, Maxillofrontale left	Not included in the analysis due to impossibility of sensible reconstruction either by reflection or by TPS because of the absence of large portions of the surface and the fossil distortion
Teshik-Tash	None	None

Zuttiyeh	Dacryon left and right, Maxillofrontale left	Medial portion of the left orbit including maxillofrontale and an inside aspect of the right orbital plate
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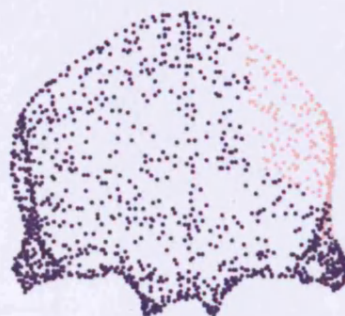
A number of fossils in the Table 5.13 are reconstructed in the same areas. Given the properties of the TPS reconstruction, this will result in biasing the reconstructed areas in favour of the reference shape, which in this analysis is the consensus shape of the recent modern individuals. Therefore, bias is introduced against the hypothesis of the individual differences in the sample and global differentiation of fossils from the recent modern humans. Any pattern of variation received with the help of the created dataset may be treated as a conservative estimate of the real differences. However, given that the reconstructions with the help of TPS function are very small, the introduced bias is expected to be small as well.

In order to verify whether the choice of the recent modern consensus shape as a reference for reconstruction of fossils affects the final result, six of the fossils of various taxonomic status, which have the largest number of missing landmarks (DV 1, Khvalynsk, La Ferrassie, Mladeč 2, Singa, Skhul V), have been additionally reconstructed using reference shape of equally varied taxonomic status: adult male Buryat individual (Bur_4587), Broken-Hill, Cro-Magnon 1 and La-Chapelle-aux-Saints. As a result, each of the reconstructed individuals has five versions of reconstructions, one of which based on the adult consensus shape. Following the same procedure as above, Procrustes distances were calculated between separate reconstructions of the same individual (25 distances) and compared with distances between the reconstructions of the respective individual and all other reconstructions in the sample (125 distances). It was expected that in case the choice

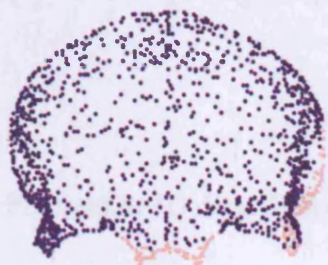
of the reference shape has significant importance for the final result, the reconstructions of one individual by different references might differ as much as individuals in the sample. However, the test has shown that in no case distances between reconstructions within one individual exceed inter-individual distances. Therefore, it is concluded that the choice of the reconstruction reference shape does not significantly affect the result and reconstructions on the basis of the recent modern human consensus shape work equally well for any of the Late Pleistocene hominins in the comparative sample, irrespective of their taxonomic status.



Brit_Brandon_765



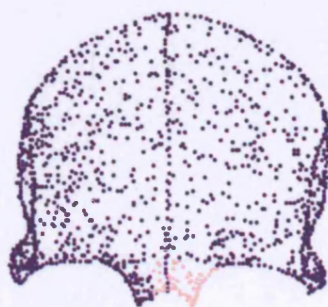
Aus_Cam_2123



Bur_4610



Eg_E6



Esk_7

Figure 5.7. 3D data. Reconstructed areas (pink) in five modern individuals.

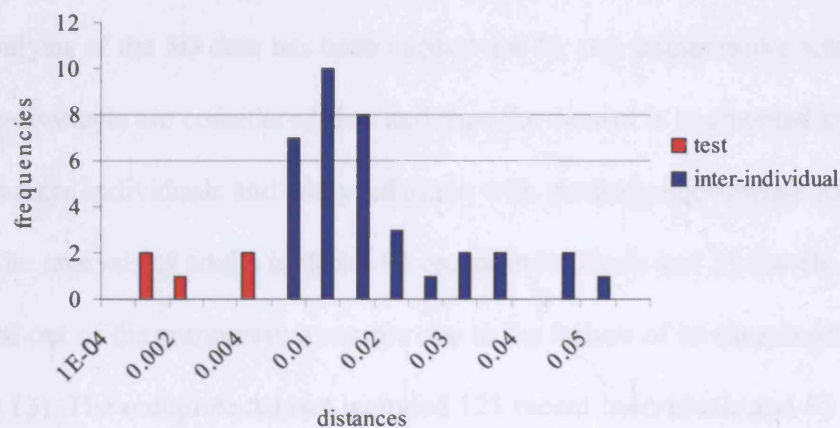


Figure 5.8. 3D data. Test of reconstruction with the help of TPS function.

The analyses

The analysis of the 3D data has been carried out for two comparative sets of individuals: adult individuals are considered first and then the dataset is augmented by the information on immature individuals and analysed again with methods appropriate for the ontogenetic data. The analysis of adults includes 91 recent individuals and 35 fossils. Only Tabun is dropped out of the comparative sample due to the failure of its meaningful reconstruction (Tab.5.13). The complete dataset included 121 recent individuals and 43 fossils.

The main purpose for both analyses is to establish morphological associations between the fossils in the North-East Eurasian sample and the known fossils from Europe, west Asia and Africa as compared to the recent modern human variation. In both cases, Relative Warp analysis plays the central role in the exploration and revealing of the pattern of morphological variation. However, the adult analysis also includes investigation of group differences and classification of fossils with the help of a permutation test and discriminant function. Multidimensional scaling is used to present an alternative view of the results of superimposition. Ontogenetic analysis uses correlation with age as a means to establish ontogenetic trajectories within different species.

Morphologically, the frontal bone may be subdivided into two regions: supraorbital area and squama. Due to the inherent features of the Relative Warp analysis, which is equivalent to Principal Component analysis (see Methods), it was expected that the analysis of the complete shape may mask finer aspects of morphology in the supraorbital region.

Therefore, two datasets were created. The first dataset included all landmarks and

semilandmarks of the complete frontal bone (see Table 3.2, Methods chapter). The second included a subset of 71 landmarks for each individual in the comparative sample (Fig.5.9) build up so as to encompass supraorbital margins, all aspects of the supraorbital relief including glabella medially, zygomatic processes laterally and the superior boundary represented by the horizontal line between two frontotemporale points. Datasets, complete frontal and the supraorbital region only, were analysed for both, adults and ontogenetic sample of individuals accordingly.



Figure 5.9. 3D data. Landmark subset for the supraorbital region.

Adults

Complete frontal bone

The analysis includes all 224 points (landmarks and semi-landmarks, see Table 3.2, Methods chapter) for each of the 91 adult individuals from nine recent populations and 34 fossils. The first five relative warps account for 73.38% of variation in the sample (Tab.5.14).

Table 5.14 3D data. Adults. Complete frontal bone: the percentage of variation described by the first five relative warps.

	<i>RW1</i>	<i>RW 2</i>	<i>RW 3</i>	<i>RW 4</i>	<i>RW 5</i>
Eigenvalue	0.279	0.163	0.065	0.052	0.019
Percent	33.93%	19.73%	8.01%	7.33%	4.37%
Total					73.37%

The first two relative warps describe the more than half of the variation (53.66%) in the sample. Recent populations and Upper Palaeolithic individuals overlap in the space of these two relative warps, whereas Neanderthals and some of the ungrouped individuals, such as Broken Hill, Singa, Qafzeh 6 and Zuttiyeh are separated from modern individuals along the second relative warp (Fig.10a). Figure 10b demonstrates trends in morphological variation explained by RW1 and RW2, which are represented by deformation of the consensus shape (TPS grid) towards the shape that is positioned three standard deviations away from it along the negative and positive directions of the respective component (dots). RW1

describes a trend from narrow and flat frontals to wide and bulging ones that is encountered in all groups of hominins. RW2, however, picks up on differences between ‘modern’ and ‘archaic’ morphology as expressed in the trend between frontal bones with slightly longer, curved squama, which is relatively wider than the flat supraorbital region in modern humans, and slightly shorter, flat squama, which has a relatively smaller width than the expanded and protruding supraorbital relief in ‘archaic’ hominins. The supraorbital relief in the ‘archaic’ shapes, however, is narrower in the cranio-caudal direction than the consensus shape. In the finer detail, which is difficult to appreciate on the two-dimensional projections of the three-dimensional pictures, the extreme ‘modern’ shape has very flat superciliary arches. The latter are manifested by two depressions lateral to glabella in the template thin plate spline grid of the consensus shape when it is transformed towards the extreme ‘modern’ target. On the contrary, the most prominent ‘archaic’ shape differs from the consensus by the especially noticeable inflation of the supraorbital trigonae. There is also a trend towards relative expansion of the temporal region in ‘archaic’ forms, which can be seen on the sagittal projection.

It is interesting to see that Skhul V and Qafzeh 6, the putative early modern humans from western Asia, cluster with Neanderthals along RW2, as well as Zuttiyeh and Singa. In other words, RW2 describes a general trend towards expanded browridges with good development of both superciliary arches and supraorbital trigonae, which are normally merged in archaic forms. In the space of the first two relative warps, Neanderthals have a range of variation, which overlaps with other Late Pleistocene hominins in the sample and is comparable to span of the variation of recent modern human populations.

Among North-Eastern Eurasian frontal bones in the analysis, only Skhodnya and Khvalynsk show closeness to the 'archaic' group, being, however, placed at the edge of recent human variation and close to Mladeč 5, Qafzeh 2, Předmostí 3 and Cro-Magnon 2. Podkumok, Sungir' 1 and Satanay are placed well within the modern human distribution and do not show any similarity to the 'archaic' morphology of the frontal bone as described by RW2.

The third and the fourth relative warps account for 15.33% of variation in the comparative sample. There is also a great overlap in distribution of recent populations in the space of these components (Fig 4.11a) with the majority of the 'archaic' hominins falling within the limits of such distribution. However, Moravian Upper Palaeolithic fossils (DV3, DV15, DV16 and Pavlov) are different from the rest of the sample along RW3 (with Gibraltar 1 forming the opposite pole of the trend in morphological variation). RW3 distinguishes between the narrow frontal bones with bulging foreheads of the Moravian sample from the relatively wide frontals with flat foreheads as expressed in Gibraltar 1 at the extreme.

Fossils such as Skhul V, Skhodnya and Khvalynsk are differentiated from the rest of the sample along RW4 (Fig. 5.11b). This relative warp shows the trend from frontals with short, rounded coronal suture, bulging forehead and relatively flat supraorbital relief towards the long and 'pointed' coronal suture where Bregma takes a posterior position, flat forehead and slightly expanded supraorbital relief. The latter morphology is unique for Skhul V, Skhodnya and Khvalynsk above all other modern and archaic individuals in the sample.

The fifth relative warp is plotted against the second relative warp in an attempt to highlight possible group differences in the sample (Fig.5.12). At its negative end, RW5 describes frontals that have relatively shorter sagittal diameter and wider transverse diameter across the middle of the frontal squama. The squama is highly curved in the sagittal projection and supraorbital relief is not prominent. At its positive end, RW5 describes slightly longer, narrow frontals with relatively wider transverse diameter across supraorbital area and elevated supraorbital relief. The expansion of the latter is most noticeable in the regions of the supraorbital trigonae. Satanay is singled out as an extreme representative of such morphology along RW5, whereas Mladeč 2 seems to be opposite to Satanay in having a short and bulging frontal that lacks any development of the supraorbital relief. Figure 5.12a shows that Satanay does not cluster with archaic hominins in the shape of the frontal. La Ferrassie and Gibraltar 1 are opposed to other Neanderthals along the fifth relative warp due to the more 'rounded' shape of the frontal squama.

In sum, the results of the present analysis have shown that Sungir' 1, Podkumok and Satanay are best associated with modern humans. Khvalynsk and Skhodnya demonstrate some level of deviation from the recent modern human morphology towards the 'archaic' shape of the frontal with particular similarities to Skhul V. The two-dimensional presentation of the results as the distribution of the sample in the space of the three pairs from the first five relative warps, shows differentiation between 'modern' and 'archaic' morphology of the frontal bone. There is considerable overlap between recent modern humans and Upper Palaeolithic fossils. A similar overlap is evident between Neanderthals and other 'archaic' hominins in the sample. For instance, Zuttiyeh, Skhul V and Qafzeh 6

seem to be closer to Neanderthals and African modern human from Singa. However, Qafzeh 1 and, to some extent, Qafzeh 2 habitually cluster with modern humans.

In the next analytical step, the significance of group differences between recent, Upper Palaeolithic and Neanderthal groups has been verified by means of the permutation test (see Methods). In order to achieve that, all landmark data after Procrustes superimposition were used and Procrustes distances were calculated between the pairs of sample means. Table 5.15 presents the *P*-values of the differences between the means of the sample. All differences are significant at the 0.01% level

Table 5.15 3D data. Adults. Complete frontal bone: Permutation test of group differences – *P*-values.

<i>Group</i>	<i>Recent modern humans</i>	<i>Upper Palaeolithic</i>	<i>Neanderthal</i>
Recent modern humans	1.0000	0.0029970	0.00099900
Upper Palaeolithic	0.0059940	1.0000	0.00099900
Neanderthal	0.00099900	0.00099900	1.0000

Given the significance of differences between Neanderthals, Upper Palaeolithic samples and recent modern humans, a question was asked whether frontal bones of the North-East Eurasian hominins in analysis would demonstrate an association with any of these groups. Two discriminant analyses is carried out on the first 16 RWs that describe about 90.3% of variation in the sample Three *a-priori* known groups and a number of ungrouped individuals are included (Tab.5.16). Prior probabilities for each group are assigned in accordance with the group size (Tab.5.16).

Table 5.16 3D data. Adults. Complete frontal bone: A-priori groups and ungrouped individuals in the Discriminant analysis.

<i>Group</i>	<i>Composition</i>	<i>Number of individuals</i>	<i>Prior probabilities</i>
Recent modern humans	9 populations	91 individuals	0.813
Upper Palaeolithic	Abri Pataud, Cro-Magnon 1, Cro-Magnon 2, Cro-Magnon 3, DV1, DV3, DV15, DV16, Mladeč 1, Mladeč 2, Mladeč 5, Pavlov, Předmostí 3	13 individuals	0.116
Neanderthal	Gibraltar 1, La Chapell aux Saints, La Ferrassie, La Quina, Neanderthal, Šal'a, Amud, Shanidar	9 individuals	0.071
Ungrouped	Broken Hill, Kanalda, Khvalynsk, Podkumok, Satanay, Skhodnya, Sungir1, Skhul V, Qafzeh1, Qafzeh2, Qafzeh6, Zuttiyeh	12 individuals	n/a

In the analysis of the first 16 RWs two significant discriminant functions are obtained that provided for the correct classification of the 96.4% cases in the original and 94.6% in the cross-validated analysis. Upper Palaeolithic group proves the least stable: four out of 13 individuals have been assigned to the recent modern group during the original test and five during the cross-validation. One individual, Předmostí 3, was mis-classified as a Neanderthal during cross-validation. Indeed, Figure 5.12 shows that even though three groups separate well in the space of the two discriminant functions, the Upper Palaeolithic group has larger spread of distribution than the two others, suggesting a different structure of the variance-covariance in the sample

The structure matrix (Tab.5.17) shows that the first discriminant function is highly positively correlated with RW2, whereas the second discriminant function is highly

positively correlated with RW3 and has smaller correlations with a number of other components, including RW6 and RW7. Figure 5.13 allows for visualisation of the distribution of the individuals in the space of these two discriminant functions. Broken Hill has the largest score along the first discriminant function apparently due to the large development of its supraorbital torus as described by the RW2. The other African fossil, Singa, is also not included into the 95% distribution area of any of the three groups in the analysis but is placed in between the Neanderthal and recent modern groups, slightly closer to the former. There is a great variation in the estimated positions of the West Asian Late Pleistocene hominins. The oldest representative from the region, Zuttiyeh, is placed together with early modern humans Qafzeh 6 and Singa in between the Neanderthal and recent modern human groups. Skhul V is placed together with Qafzeh 6 and Zuttiyeh along D1 but hugely deviates along D2 towards the Upper Palaeolithic group. To the contrary, Qafzeh 1 and Qafzeh 2 are both placed within the intersection region between recent and Upper Palaeolithic modern humans.

Table 5.17 3D data. Adults. Complete frontal bone: Structure matrix for discriminant analysis of 16RWs.

<i>Variable</i>	<i>Function 1</i>	<i>Function 2</i>
RW1	-0.053	.119(*)
RW2	.571(*)	-0.116
RW3	0.12	.575(*)
RW4	-.041(*)	-0.005
RW5	0.081	.081(*)
RW6	0.158	-.254(*)
RW7	-0.004	-.233(*)
RW8	0.058	.105(*)

RW9	-.073(*)	0.011
RW10	0.041	-.082(*)
RW11	0.06	.157(*)
RW12	-.094(*)	-0.075
RW13	-.090(*)	-0.011
RW14	-0.017	.138(*)
RW15	-0.015	.133(*)
RW16	-0.084	.152(*)

(*) denotes significant correlation with the respective component; bold font highlights the largest values of such correlation

In this picture, the North-East Eurasian hominins distribute as follows: Sungir' 1 is plotted within the recent modern human variation just at the edge of the overlap with the Upper Palaeolithic group. At the same time, Podkumok is placed well within the distribution of the Upper Palaeolithic individuals. Taking into account that Sungir' 1 comes from a known Upper Palaeolithic context and has a firm radiocarbon date, the grouping of Podkumok with other European Upper Palaeolithic individuals gives additional weight to its possible Upper Palaeolithic origin. Satanay and Skhodnya are placed in between recent modern and Neanderthal groups, very close to Zuttiyeh, Qafzeh 6 and Singa along D1 but separating from them and from each other along D2. Khvalynsk is very close to the area of the 95% distribution of Neanderthals.

Mahalanobis distances between some of the ungrouped individuals and the centres of their first predicted groups are presented in the Table 5.18. The maximum distance within the recent modern sample, Upper Palaeolithic sample and Neanderthals are given for the comparison.

Table 5.18 3D data. Adults. Complete frontal bone: Classification results for the ungrouped individuals.

	<i>First predicted group</i>	<i>Squared Mahalanobis distance to centroid*</i>
<i>Maximum distance within the recent modern group to its centre</i>		10.79
<i>Maximum distance in the Upper Palaeolithic group to its centre for the exception of Předmostí 3</i>		5.15
<i>Maximum distance within the Neanderthal group to its centre</i>		4.62
<i>Předmostí 3</i>	UP	14.61
<i>Broken Hill</i>	NEA	9.49
<i>Singa</i>	NEA	9.29
<i>Skhul V</i>	UP	16.59
<i>Qafzeh 1</i>	MOD	1.36
<i>Qafzeh 2</i>	MOD	4.00
<i>Qafzeh 6</i>	NEA	9.36
<i>Zuttiyeh</i>	MOD	13.74
<i>Podkumok</i>	UP	1.88
<i>Sungir 1</i>	MOD	0.56
<i>Khvalynsk</i>	NEA	4.98
<i>Satanay</i>	MOD	14.07
<i>Skhodnya</i>	MOD	15.49

* Cases with large values of Mahalanobis distance from their group mean can be identified as outliers.

Předmostí 3 also behaves as an outlier of the Upper Palaeolithic group. Skhul V and Zuttiyeh have very large distances to the centres of the predicted groups and cannot be assigned to them. The same may be said about Skhodnya and Satanay, whose distances to the recent modern group exceed the maximum distance within the recent modern human

sample to its respective centre. Khvalynsk is classified as a Neanderthal. Only Podkumok and Sungir' 1 fit well within the modern human morphological variation with Sungir' 1 being most similar to recent modern humans and Podkumok – to the European Upper Palaeolithic sample. As a result, Satanay, Skhodnya and Khvalynsk may be differentiated from modern humans. However, it is also possible that the variation among these hominins cannot be resolved by comparison with the three *a-priori* groups in the analysis

Multidimensional scaling has been performed on Procrustes distances between all individuals in a sample of consensus shapes of each of the recent human population and all adult fossils. In total, 43 individuals (including nine consensus shapes) were included in the analysis. The three-dimensional projection of the data has stress values of 12.96% Stress (D-hat Raw stress in STATISTICA) and 0.0837 SStress (D-hat Stress in STATISTICA), which indicate that this projection gives a satisfactory representation of the original distances (Johnson and Wichern, 2002). Figure 5.14 shows the projection of the original configuration to the space of the three MDS axes. Multidimensional scaling results repeat the results of the Relative Warp analysis in a number of aspects. For instance, modern and 'archaic' individuals differ along the first dimension of scaling. However, Neanderthals cluster together in the first dimension and, with the exception of Neanderthal itself, along the second dimension. MDS of the Procrustes distances, therefore, provides for a more explicit picture of the difference of Neanderthals as a group from other Late Pleistocene fossils in the sample than the one received in the Relative Warp analysis.

Predictably, Broken Hill has the largest distances from other individuals in the sample as reflected in the first and second dimensions. Fossils such as Skhul V and Qafzeh 6 overlap with Neanderthals, whereas Zuttiyeh is placed in between the Neanderthals and modern

humans in the first dimension. Differences between some of the Upper Palaeolithic individuals and the consensus shapes of the recent human populations are reflected in the third dimension of the scaling. For instance, all Dolní Věstonice individuals, Pavlov, Předmostí 3, Cro-Magnon 1 and Cro-Magnon 2 take positive values along the third dimension. Abri Pataud is close to zero, whereas all the recent consensus shapes take negative values in the same dimension. Cro-Magnon 3 and all Mladeč individuals cluster together with the recent consensus shapes.

Within the outlined picture, Skhodnya, Khvalynsk and Satanay are relatively close to each other along the first and the second dimension but separate along the third dimension. They are relatively far away from the recent individuals along the second axis and intermediate between 'archaic' fossils and recent groups along the first one. Skhodnya and Khvalynsk maintain differences from the recent individuals along the third dimension being closer to Předmostí 3 and other Upper Palaeolithic fossils from the same sub-group, whereas Satanay is slightly closer to the recent populations and such fossils as Mladeč 2 and 5 along the third axis. Podkumok is shown to be similar to modern individuals in general (first dimension) and the majority of the Upper Palaeolithic fossils along the other two dimensions, whereas Sungir' 1 is very similar to the recent consensus shapes. However, the consensus shape of the Australian population has the absolutely smallest Procrustes distance with Sungir' 1 frontal (0.0018), with Teita consensus shape being the next closest (0.0021). The range of distances between Sungir' 1 and recent modern human populations goes up to 0.0076 with Buryats, whereas with fossils cover the range from 0.0056 with Mladeč 5 to 0.0256 with Broken Hill

It is interesting to see that Mladeč 2 clusters together with Neanderthals instead of the Upper Palaeolithic modern humans in all dimensions. Mladeč 2 has also shown some similarities with Neanderthals in the Relative Warp analyses, where it was placed at the boundary between modern and ‘archaic’ groups of hominins along RW2. Figure 5.14a and b compares Mladeč 2 with a ‘typical’ Upper Palaeolithic fossil Cro-Magnon 1 and a ‘typical’ Neanderthal – La Ferrassie (here ‘typical’ refers to the position of the respective fossils among alike individuals). In all cases, Mladeč 2 is represented by dots, whereas Cro-Magnon 1 and La Ferrassie are represented by the TPS grid deformed so as to fit the Mladeč 2 landmark configuration. In comparison to Cro-Magnon 1, Mladeč 2 has a flatter frontal with relatively expanded anterior end and a narrower posterior part of the squama (Fig.5.15 a and b). There is also some degree of deformation in Mladeč 2 in the right posterior aspect of the frontal squama, which is highlighted in the picture with the double magnification of differences (Fig.5.15 c). The relative flatness of the frontal and the expansion of the supraorbital region align Mladeč 2 with Neanderthals even though it is lacking supraorbital ridges as seen in comparison with La Ferrassie (Fig.5.15 d and e). In other words, the La Ferrassie grid is only deformed so as to account for the lack of supraorbital ridges, a slightly higher curvature of the frontal squama and just marginally narrower anterior and posterior aspects of the frontal in Mladeč 2. DV3 also deviates from the majority of the modern individuals in the first dimension in a direction opposite to Mladeč 2. Figure 5.16 compares DV3 with Cro-Magnon 1. As in the previous case, DV3 is represented by dots and Cro-Magnon 1 by the TPS grid bent to fit the DV3 configuration. In comparison with Cro-Magnon 1, DV3 has considerably narrower zygomatic processes and ‘sloping’ sides of the coronal suture (Fig.14.16a). It also has a steeper supraglabellar region (Fig.5.16b).

In total, the Multidimensional scaling confirms the Relative Warp and Discriminant analyses results. Given that Multidimensional scaling is not affected either by the presence of outliers or by the influence of groups with large sample size, it is a more or less independent representation of the Procrustes distances. The latter, however, do not allow for the interpretation of the shape trends in the data if taken by themselves.

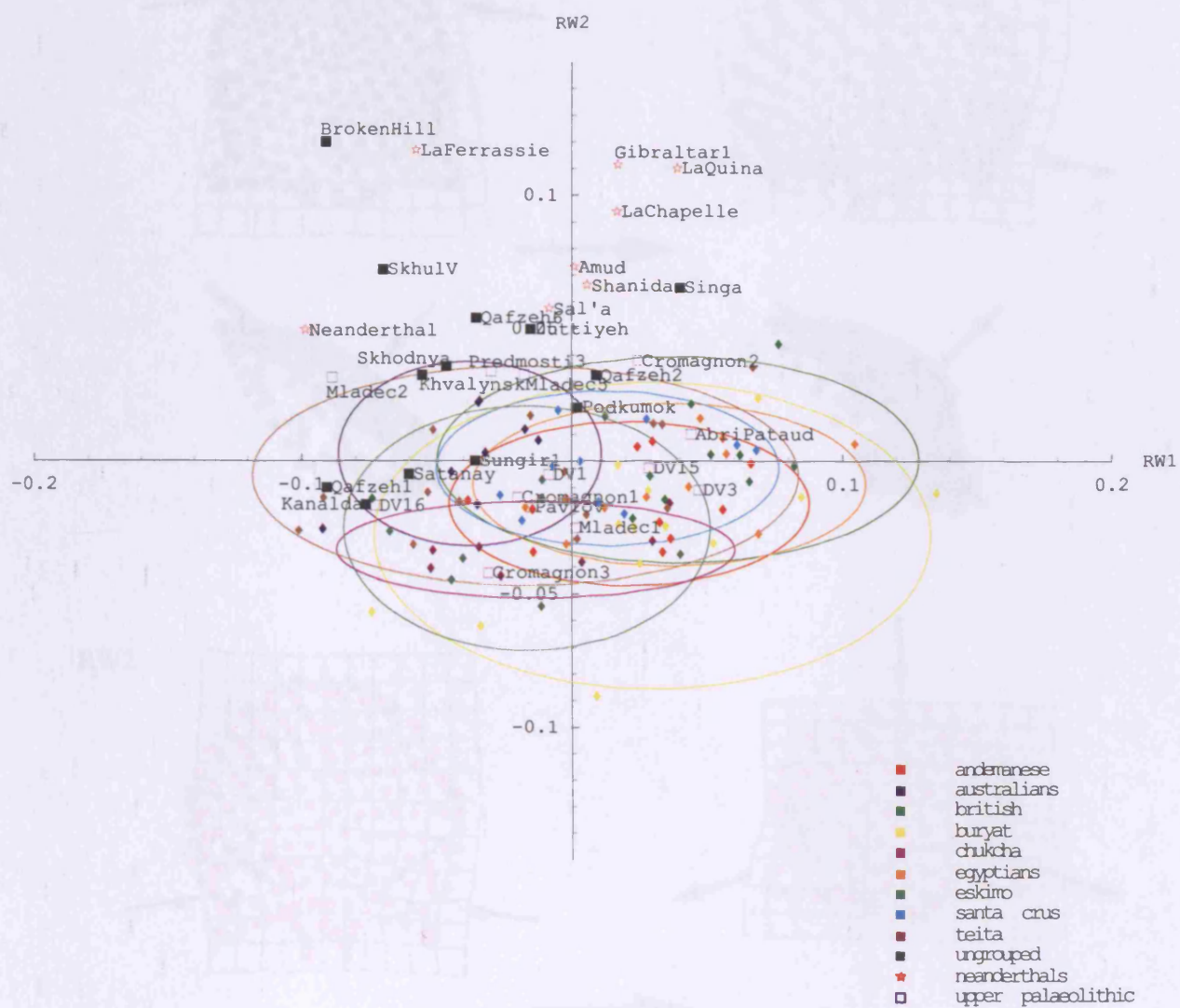


Figure 5.10a. 3D data for the complete frontal bone. Adults. First and second relative warps: distribution of individuals.

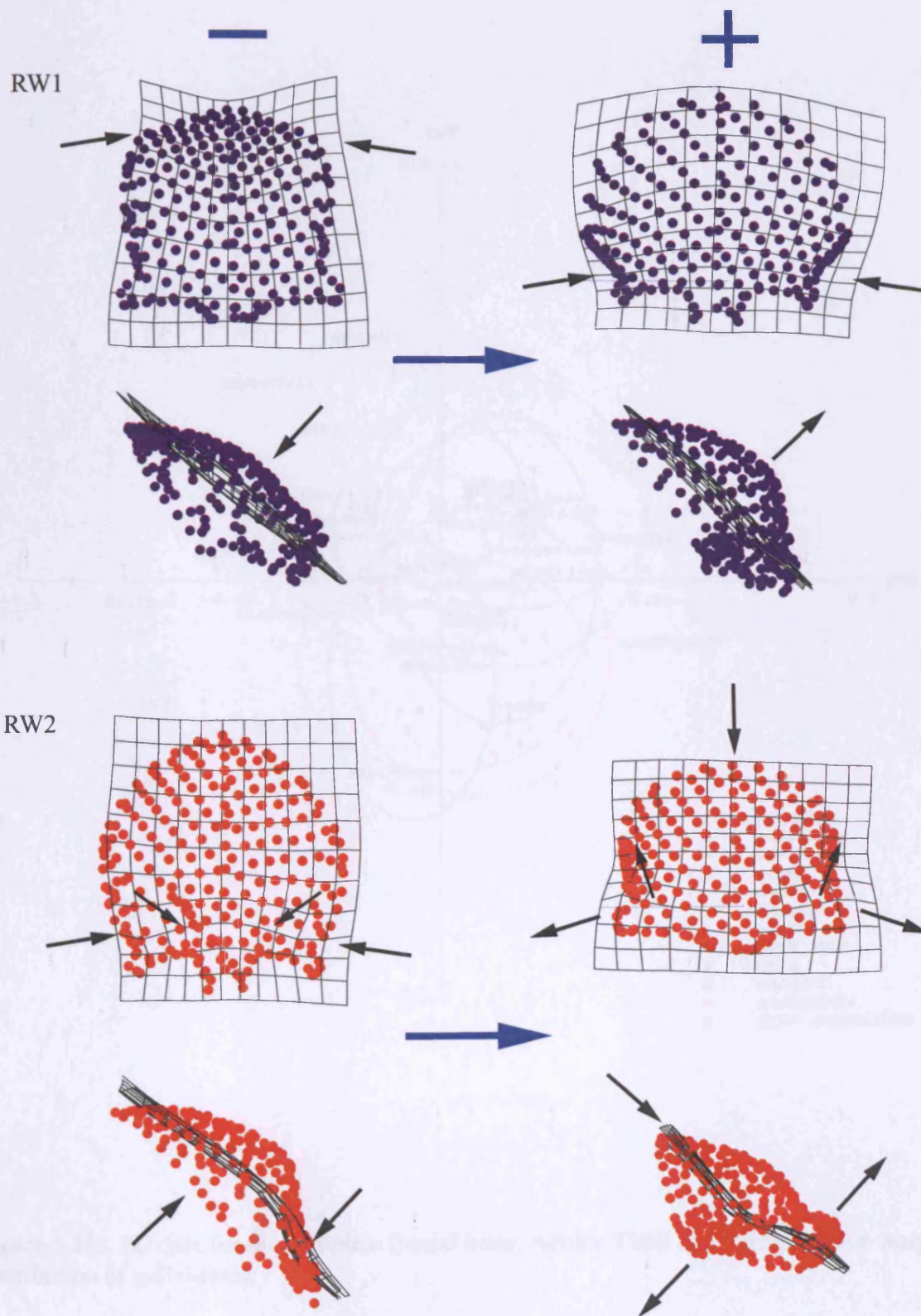


Figure 5.10b. 3D data for the complete frontal bone. Adults. First and second relative warps: morphological trends described. TPS transformation of the consensus shape grid towards the target of a shape three standard deviations away from the consensus.

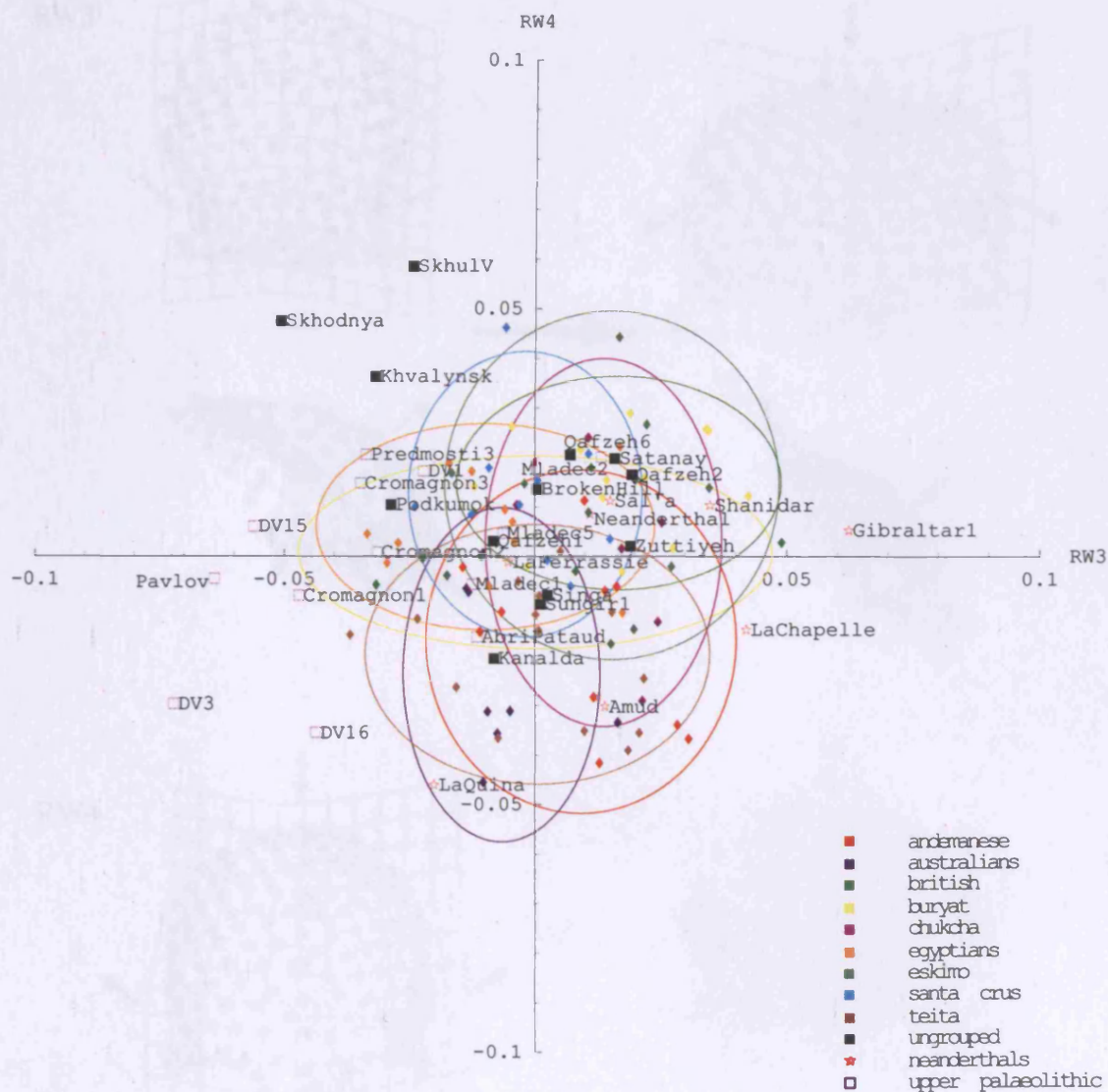


Figure 5.11a. 3D data for the complete frontal bone. Adults. Third and fourth relative warps: distribution of individuals.

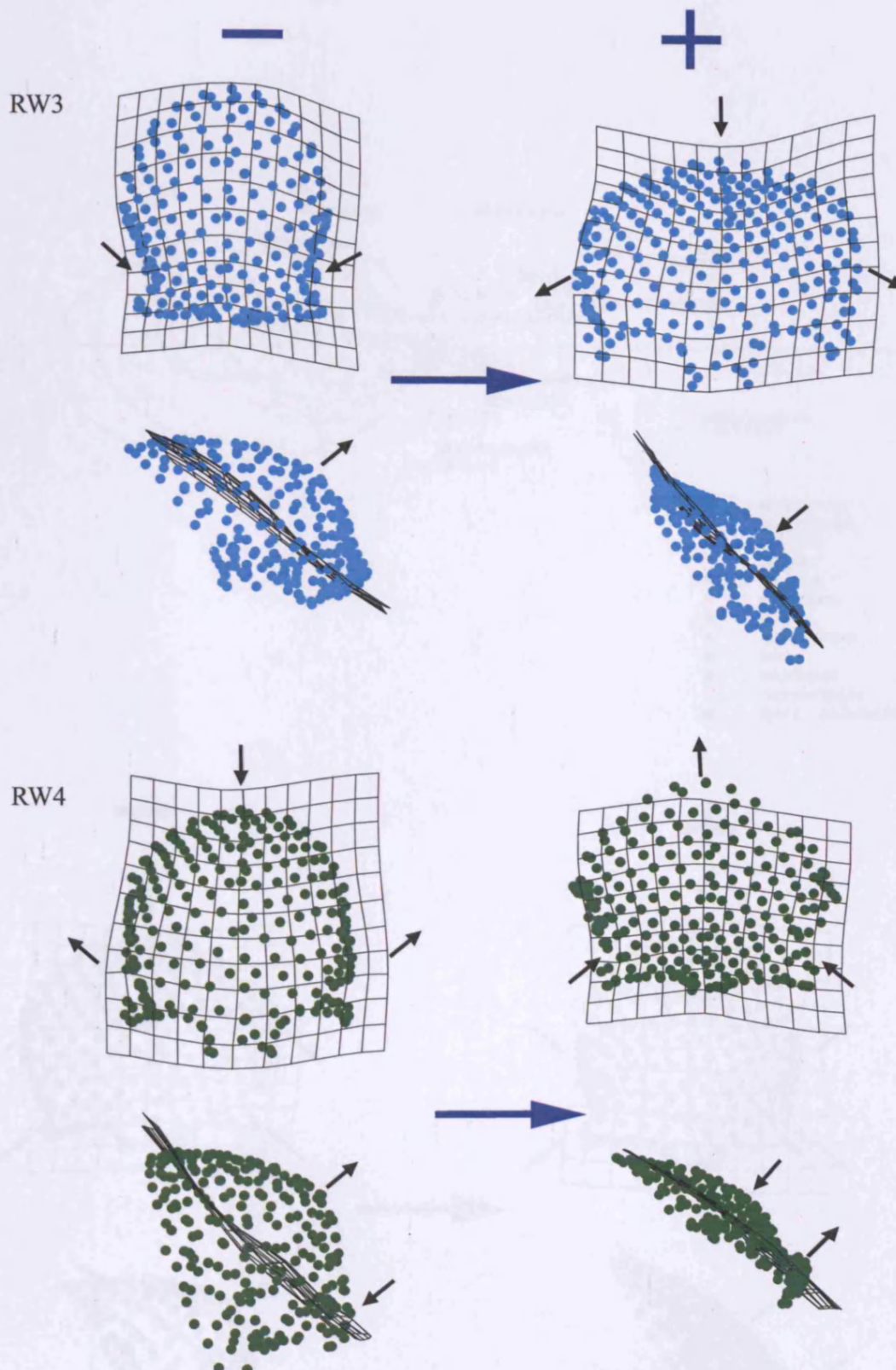


Figure 5.11b. 3D data for the complete frontal bone. Adults. Third and fourth relative warps: morphological trends described. TPS transformation of the consensus shape grid towards the target of a shape three standard deviations away from the consensus.

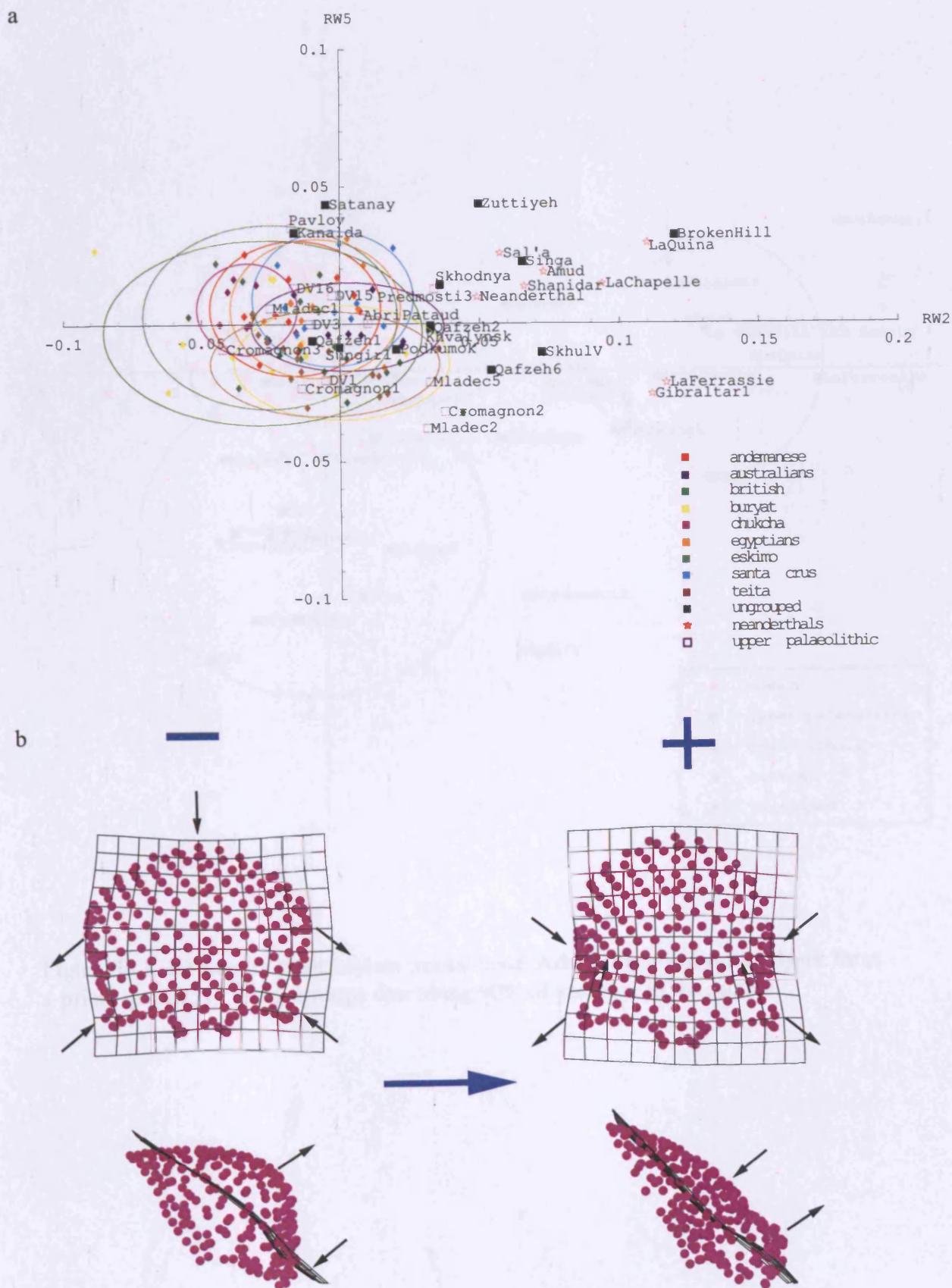


Figure 5.12. 3D data for the complete frontal bone. Adults. Second and fifth relative warps: a) distribution of individuals; b) morphological trend described by RW5.



Figure 5.13. 3D data for the complete frontal bone. Adults. Discriminant analysis: three a-priori groups, 16 relative warps describing 90% of variation in the sample.

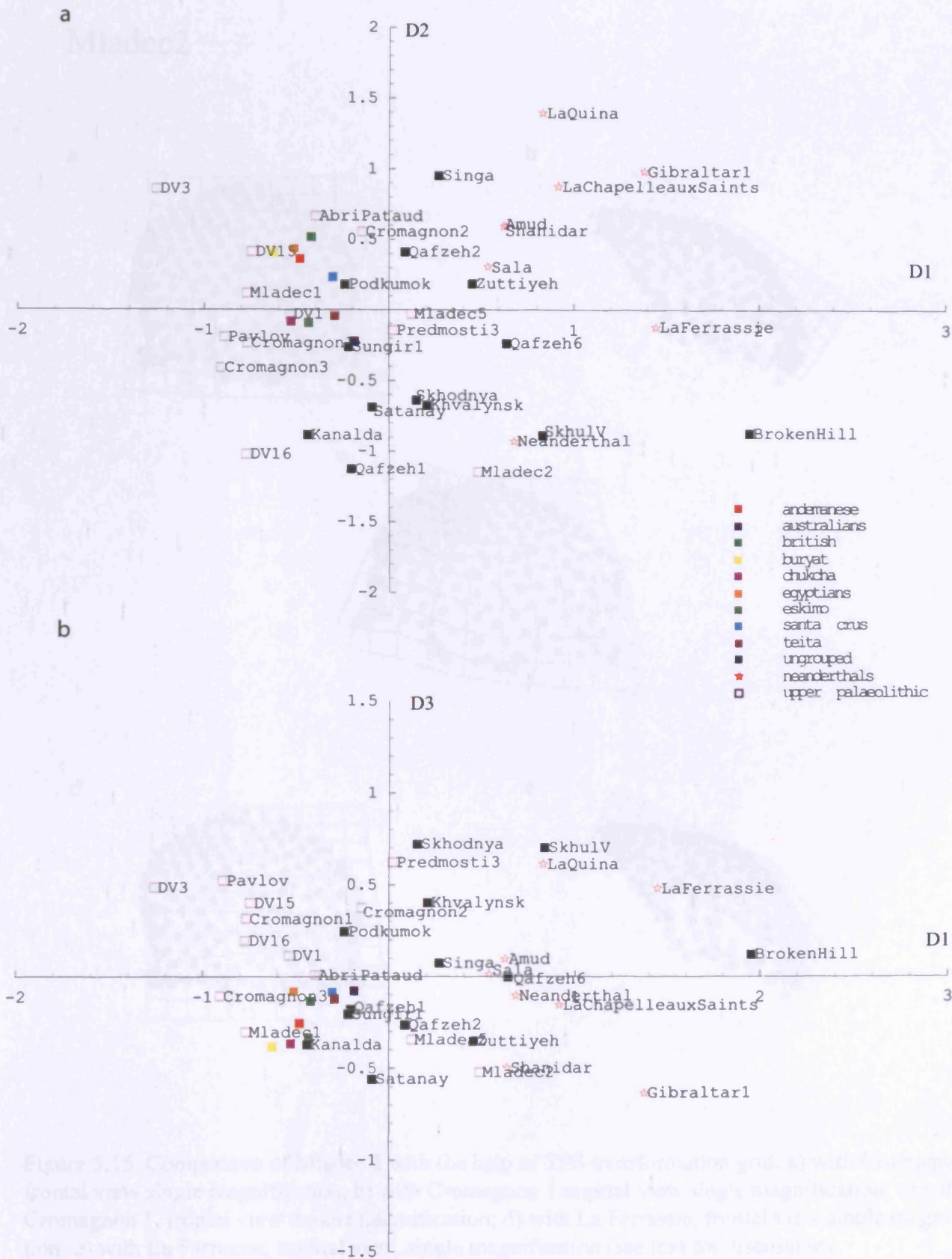


Figure 5.14. 3D data for the complete frontal bone. Adults. Results of the Multidimensional scaling: a) First and second dimensions; b) first and third dimensions.

Mladec2

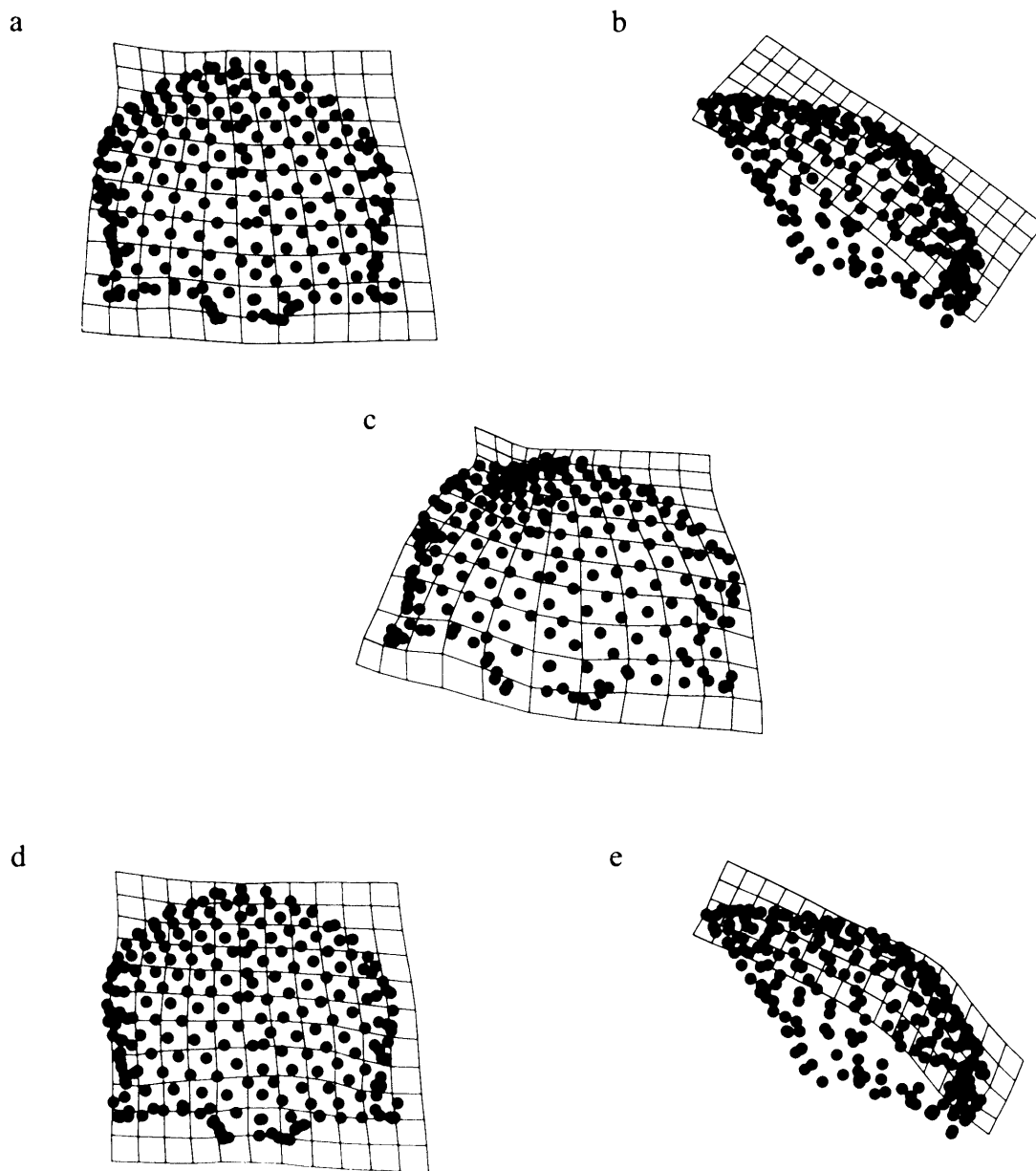


Figure 5.15. Comparison of Mladec 2 with the help of TPS transformation grid: a) with Cromagnon 1, frontal view single magnification; b) with Cromagnon 1 sagittal view single magnification; c) with Cromagnon 1, frontal view double magnification; d) with La Ferrassie, frontal view single magnification; e) with La Ferrassie, sagittal view, single magnification (see text for discussion).

DV3

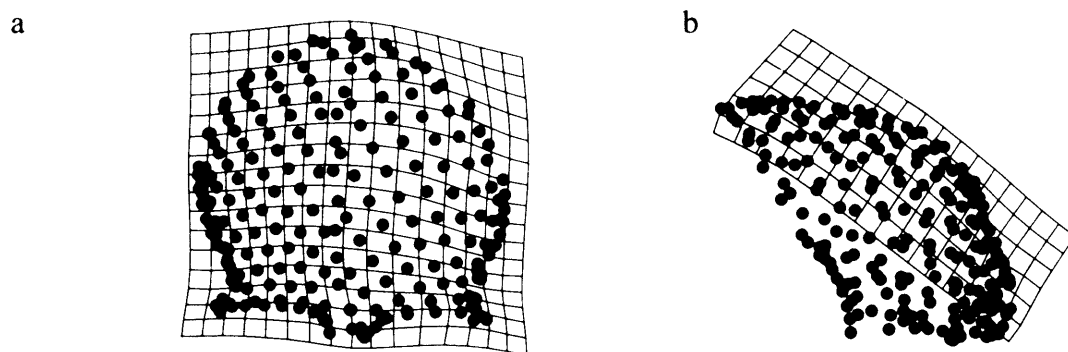


Figure 5.16. Comparison of DV 3 with the help of TPS transformation grid: a) with Cromagnon 1, frontal view single magnification; b) with Cromagnon 1 sagittal view single magnification (see text for discussion).

Supraorbital region

The analysis of the supraorbital region has been designed in order to concentrate on a single anatomical region that may potentially provide for a better resolution between taxa. Smith and Ranyard (1980) described characteristic Neanderthal browridges as an osseous bar projecting from the frontal squama at the inferior border of the frontal bone and arching from glabella laterally over each orbit to the frontozygomatic suture. There is a depression in the torus above the glabella and the torus continues laterally into the so-called lateral orbital pillars (Smith and Ranyard, 1980) .

The analysis included 91 recent adult individuals from nine populations and 34 fossils. The primary exploration of the morphological trends in the sample and the comparative position of five out of nine North-East European fossils have been carried out with the help of Relative Warp Analysis. The first four relative warps account for 70.78% of the variation in the sample (Tab.5.19).

Table 5.19 3D data. Adults. Supraorbital region: Percent of variation described by the first five relative warps in the analysis of supraorbital region for adults only.

	<i>RW1</i>	<i>RW 2</i>	<i>RW 3</i>	<i>RW 4</i>	<i>RW5</i>
Eigenvalue	0.259	0.112	0.077	0.037	0.029
Percent	35.59%	15.43%	10.62%	5.08%	4.06%
Total					70.78%

The scatter of individuals in the space of the first two relative warps (Fig.5.17a) shows that the largest variation is found between modern humans and 'archaic' hominins due to the absence of browridges in the former (RW1). Figure 5.17b presents TPS transformation grids for the trend between the 'archaic' and 'modern' morphological states. As in previous analyses, the TPS grid here represents the consensus shape in the sample (template), which is bent towards the landmark configuration of the farthest representative shape along the respective relative warp (target). It is possible to see that the 'archaic' forms have anteriorly projecting browridges, which coincide with the cranio-caudal 'squashing' of the whole supraorbital region. Glabella is positioned anteriorly to Nasion and there is no apparent subdivision between portions of the supraorbital relief.

The supraorbital region of the 'archaic' forms in the analysis has rounded outline in the superior view (Fig.5.17b). In other words, zygomatic processes and frontotemporale areas are positioned posterior position to the projecting glabella and about two thirds of the adjacent orbital lengths in the transverse plane. This uniform structure corresponds with the definition of the supraorbital torus. In contrast, 'modern' morphology is characterised by a high and transversely flat supraorbital region that does not sweep back laterally. At its extreme, glabella is not anterior to nasion. On the transverse projection of the modern shape, one can also see the presence of small elevations of the superciliary arches (Fig.5.17b).

Broken Hill has the most prominent browridge within this pattern, whereas Neanderthals overlap with Singa, Qafzeh 6, Skhul V, Zuttiyeh and Předmostí 3. Skhodnya and Khvalynsk also fall within this group of individuals.

It is interesting to see that, with the exception of Předmostí 3, the majority of the Upper Palaeolithic individuals fall at the boundary with the 'archaic' group but overlap with recent individuals in general and with Australians in particular. Podkumok and Sungir' 1 are placed within this scatter of individuals, whereas Satanay has slightly more prominent supraorbital relief.

RW2 differentiates some of the Neanderthals. Figure 5.17b shows that RW2 mainly picks up on the trend between forms with different angles of inclination of the supraorbital region. La Quina, La Ferrassie, Gibraltar 1 and DV3 have obtuse angles of the supraorbital region in their sagittal projection, whereas Skhul V and Zuttiyeh have acute inclination angles of supraorbital region in their respective sagittal projections. RW2 also highlights size of the orbits relatively transverse diameter across frontotemporale as well as the general outline of the supraorbital region in the frontal view. Thus, forms with forwardly sloping supraorbital regions also have wider orbits with relatively straighter outline of the supraorbital margins (such as in Skhul V), whereas forms with the obtuse angle of the supraorbital region in its sagittal projection, also have more rounded orbits that appear to have relatively smaller transverse diameters in comparison to the wider diameter across frontomalarotemporale areas. The combination of the latter shape with the projecting and rounded supraorbital torus as described by the first relative warp distinguishes La Quina, La Ferrassie, Gibraltar 1 and Amud Neanderthals, whereas La Chapelle aux Saints, Shanidar, Neanderthal and Šal'a do not display large deviation along the second relative warp and overlap with other Late Pleistocene fossils in the analysis in the shape of their supraorbital relief.

It was expected that all Neanderthals would demonstrate considerable differences from the majority of other Late Pleistocene hominins due to their distinctive 'double arch' shape of the supraorbital torus as described by Smith and Raynard (1980). However, the first two relative warps in the analysis demonstrated large overlap of Neanderthals and other Late Pleistocene fossils in the analysis. Neanderthals overlap in the degree of the projection of the supraorbital region as described by RW1 with such fossils such as Singa, Skhodnya, Skhul V and Khvalynsk and show relatively large variation along RW2. This result does not undermine the differentiation of Neanderthals as a group from other Late Pleistocene fossils. However, it suggests that the unique 'double arched' supraorbital torus in Neanderthals is somehow illusive in the face of variation within the group.

In sum, the present analysis highlights the following comparative aspects of the morphology: a) modern humans (including the majority of the Upper Palaeolithic fossils and recent populations) differ from the earlier hominins, including the west Asian early modern humans from Skhul V and Qafzeh 6 in the shape of the supraorbital region; b) not all west Asian fossils have large browridges: Qafzeh 1 and Qafzeh 2 fall within the modern human variation; c) not all Upper Palaeolithic fossils cluster together with recent modern humans: Předmostí 3 is found to have very large development of supraorbital relief, comparable, for example, with Neanderthal; d) Neanderthals vary in browridge morphology and fail to form a solid group when compared with the variation in modern humans and other 'archaic' forms.

The majority of the Upper Palaeolithic modern humans in the sample, with the exception of DV1, demonstrate differences from other individuals in the sample along the third relative warp (Fig.5.18a). Some of them, for example, Cro-Magnon 3, Předmostí 3, DV15 and

DV3, completely fall out of the main spread of recent modern humans and deviate towards Skhul V. RW3 highlights differences between browridges of Skhul V which are relatively narrow in the cranio-caudal direction, and the high and generally larger ones in Broken Hill (Fig.5.18b). There are no other noticeable differences in morphology. To the contrast, most Neanderthals, with the exception of Šal'a, show higher browridges by assuming positive values along RW3 and totally overlap with recent human variation along this component.

The variation of the recent modern humans along the fourth relative warp encompasses variation in the majority of the fossil hominins. RW4 describes the trend between individuals with a relatively narrow interorbital distance, deep glabella and wider orbits (such as in DV3, DV15 and some Chukcha and Eskimo individuals) and individuals with projecting glabella, relatively wide interorbital distance, and relatively small and rounded orbits, such as in Qafzeh 1 and Podkumok (Fig 4.18 a and b). Upper Palaeolithic individuals demonstrate a range of variation along RW4, comparable to the complete sample of recent individuals. On the other hand, most Neanderthals (with the exception of La Chapelle aux Saints that scores high along RW4) show average or narrow relative interorbital distance.

The fifth relative warp discloses additional information about the variation structure in the sample. It is plotted against RW1 in Figure 5.19a in an attempt to highlight group differences, if any, between modern and archaic individuals in the sample. At its negative values, RW5 describes individuals with wide interorbital distances where the nasion is as far forward as the glabella, and the area above the glabella runs quickly backwards creating an angle with the vertical forehead (Fig.5.19b). Given the widening of the glabella, orbits take a more lateral position without compromising their size. At its positive values, RW5 is

correlated with narrow interorbital distance coupled with the relatively deeper position of nasion and anterior expansion of the whole area above glabella. Here, the inferior lateral corners of supraorbital margins are rounded and the position of the orbits is shifted medially.

Most Neanderthals overlap with modern human variation along this component. However, with the exception of Šal'a, they have positive scores along RW5 with Shanidar being the farthest along RW5. Among all individuals in the sample, Qafzeh 6 scores the top positive value along RW5 thus demonstrating the extreme variant of the combination between the relatively narrow interorbital distance, rounded orbits and a relatively deep position of glabella and nasion. Upper Palaeolithic humans overlap with the recent modern populations. A few of them, such as Pavlov, Předmostí 3, DV1 and Mladeč 2 show a trend opposite to Neanderthals: they have relatively straighter orbits and wider interorbital distance when compared to the consensus shape (Fig 4.19b). None of the North-East Eurasian fossils fall outside the range of the recent modern human variation along the fifth relative warp concentrating mostly close to its centre.

In conclusion, some of the North-East Eurasian fossils in the present analysis, namely Skhodnya and Khvalynsk, show relatively large development of supraorbital relief, comparable with forms such as Singa, Neanderthal and Předmostí 3. However, this relatively large development of the supraorbital relief is not due to overall robusticity (Lahr, 1996) at least in the case of Khvalynsk, which represents a relatively gracile and small individual. Podkumok and Sungir' 1 fall within the variation of the Upper Palaeolithic individuals. Satanay shows just a little larger development of the supraorbital region than encountered within the modern human sample comparable, for example, with

Pavlov by the prominence and to Zuttiyeh, DV15 and 16 in morphological aspects described by the second relative warp, such as relatively acute angle of inclination of the supraorbital region in the sagittal projection and relatively wider and straighter supraorbital margins.

The significance of distances between the means of Upper Palaeolithic, Neanderthal and recent modern human groups has been tested by the permutation test (see Methods). In order to achieve that, Procrustes distances were calculated between pairs of group means. Table 5.20. presents *P*-values of the differences between the groups. All differences are significant at the 0.01% level.

Table 5.20 3D data. Adults. Supraorbital region: Permutation test of group differences – *P*-values.

<i>Group</i>	<i>Recent modern humans</i>	<i>Upper Palaeolithic</i>	<i>Neanderthal</i>
Recent modern humans	1.0000	0.00099900	0.00099900
Upper Palaeolithic	0.00099900	1.0000	0.00099900
Neanderthal	0.00099900	0.00099900	1.0000

As in the case with the complete frontal bone, the next analytical step involved Discriminant analysis for all adult samples including three *a-priori* known groups (recent humans, Upper Palaeolithic and Neanderthals). As for the complete frontal bone, the discriminant analysis was carried out for 18 RWs that describe about 90.3% of variation in the sample. The group composition and prior probabilities for the groups are identical to those in the Discriminant analysis of the complete frontal bone (Tab.5.16).

The analysis of the first 18 RWs yielded two significant discriminant functions (that provide for 96.4% of the correct classification in the original analysis and 94.6% of the

correct classification during cross-validation. The first discriminant function largely emphasises the influence of the first relative warp (Tab.5.21), whereas a number of other relative warps are less important. In other words, the first discriminant function mostly shows the morphological trend between the forms with a tall and flat supraorbital region and forms with a ‘squashed’ and projecting supraorbital region. The first discriminant function separates Neanderthals from both Upper Palaeolithic and recent modern humans. The second discriminant function has the largest correlation with RW3 (height of the supraorbital region) and RW6 (Tab.5.21). However RW14, RW12, RW5 and a number of other relative warps also have comparable contribution. Recent and Upper Palaeolithic humans are separated along this discriminant function.

Table 5.21 3D data. Adults. Supraorbital region: Pooled within-groups correlations between Relative Warps and standardized canonical discriminant functions for the analysis of 18RWs.

<i>Variable</i>	<i>Function 1</i>	<i>Function 2</i>
RW1	-.603(*)	0.439
RW9	-.183(*)	0.002
RW4	-.076(*)	0.034
RW13	-.075(*)	-0.071
RW2	.057(*)	0.048
RW18	-.025(*)	-0.016
RW3	0.083	.393(*)
RW6	0.13	.366(*)
RW14	-0.04	.251(*)
RW10	-0.061	.235(*)
RW5	0.096	.218(*)
RW8	-0.036	-.205(*)

RW11	0.035	.143(*)
RW15	0.03	-.068(*)
RW16	0.057	.066(*)
RW12	0.025	-.045(*)
RW7	0.016	-.038(*)
RW17	-0.01	-.026(*)

* Largest absolute correlation between each variable and any discriminant function.

Figure 5.20 demonstrates the scatter of individuals in the space of the two discriminant functions. The most noticeable feature of the present analysis is the large spread of distribution of the Upper Palaeolithic individuals, which is mostly brought about by the large deviation of DV16, Pavlov, DV15, Cro-Magnon 3, Předmostí 3 and DV3 along the second discriminant function and Předmostí 3 along the first one. Such a large distribution in the Upper Palaeolithic sample may point to its different variance-covariance structure than the one found in recent modern humans and Neanderthals. In this context, it is interesting to see that Kanalda, an early Holocene fossil from Australia, falls within the recent modern human variation thus conforming to the relatively narrow morphological variation within this group and relative robustness of classification results.

The other interesting point of the present analysis is that Khvalynsk, Zuttiyeh and Singa fall within the 95% distribution interval of the Neanderthals with Skhodnya and Qafzeh 6 are also placed close to the Neanderthal group and classified as Neanderthals (Table 5.22).

Sungir1 has been classified as a recent modern human, but, consistently with the results on the complete frontal, it falls within the overlap with the Upper Palaeolithic group.

Podkumok has been classified as Upper Palaeolithic. Satanay, Skhul V and Předmostí 3

were assigned to either recent or Upper Palaeolithic modern humans (Tab.5.22). However, their distances to the centres of the respective groups are very large so that they fall out of the 95% of the group distribution (Fig.5.20). As in the analysis of the complete frontal bone, there is a large spread of variation among the West Asian fossils: whereas it might be not very surprising that Zuttiyeh has been classified as a Neanderthal by the morphology of the supraorbital relief, the classification of the early Modern human Qafzeh 6 as a Neanderthals is surprising. However, Qafzeh 6 has a relatively large distance to the centre of the Neanderthal group (Tab.5.22) and hence may be deemed an outlier to it. The position of Skhul V is most possibly irresolvable in the space of the three *a-priori* groups in the analysis. It stays unique in combination of the morphological features within the comparative sample of individuals. Qafzeh 1 and 2 have again been placed within modern human distribution, with the former looking more as Upper Palaeolithic and latter as a recent modern human. Unlike the majority of the Upper Palaeolithic fossils in the analysis, Předmostí 3 consistently deviates towards more ‘archaic’ morphology of the frontal bone. In this respect Satanay is similar to Předmostí 3 in the morphology of the browridges: neither of them is a Neanderthal but they are also very different from the modern humans (Tab.5.22).

Table 5.22 3D data. Adults. Supraorbital region: Distances to the centres of the first predicted groups in the Discriminant analysis of the 18RWs.

	<i>First predicted group</i>	<i>Squared Mahalanobis distance to centroid*</i>
<i>Maximum distance among recent modern individuals to the centre of the group</i>		7.107
<i>Maximum distance among Upper Palaeolithic individuals to the centre of the group (excluding Předmostí 3)</i>		7.92
<i>Maximum distance among Neanderthals to the centre of the group</i>		5.61

<i>Broken-Hill</i>	<i>NEA</i>	7.168
<i>Singa</i>	<i>NEA</i>	2.647
<i>Skhul V</i>	<i>UP</i>	12.222
<i>Qafzeh 6</i>	<i>NEA</i>	7.812
<i>Zuttiyeh</i>	<i>NEA</i>	3.282
<i>Předmostí 3</i>	<i>UP</i>	15.613
<i>Podkumok</i>	<i>UP</i>	5.445
<i>Sungir</i>	<i>MOD</i>	0.508
<i>Khvalynsk</i>	<i>NEA</i>	1.75
<i>Satanay</i>	<i>MOD</i>	14.058
<i>Skhodnya</i>	<i>NEA</i>	8.279

Representation of the inter-individual Procrustes distances with the help of Multidimensional scaling provides for further insights into the structure within the comparative sample. Present Multidimensional scaling analysis was built upon the matrix of Procrustes distances between the consensus shapes of each of the nine recent human populations and all adult fossils in the analysis (43 shapes) for the browridge data subset (see above). The best low-dimension fit was achieved for four dimensions with the stress (D-hat Raw stress in STATISTICA) equal to 7.88% and SStress (D-hat Stress in STATISTICA) to 0.065 (Johnson and Wichern, 2002). Figure 5.21 demonstrates the distribution in space of these four dimensions. A good group resolution is provided by plotting the first and third dimensions (Fig.5.21a). First of all, there is a dramatic difference between all the modern and ‘archaic’ individuals in the sample, summarised in the first dimension of the scaling. Second, there is a noticeable variation among the Upper

Palaeolithic individuals due to clustering of Předmostí 3 with the ‘archaic’ hominins on one hand and the spread of variation among the Upper Palaeolithic individuals along the third dimension, as opposed to a tighter clustering of Neanderthals and recent human consensus shapes with each other. In this space, Broken Hill has the largest distance from the rest of the comparative sample. Skhodnya and Khvalynsk confirm their association with Neanderthals and other ‘archaic’ hominins, such as Singa, Skhul V and Zuttiyeh. The intermediate position of Qafzeh 6 and Satanay is also corroborated by the first and third dimensions of the scaling. Podkumok and Sungir’ 1 find themselves associated with the modern humans. The present picture also agrees with the earlier observation on the large variation within the west Asian sample of fossils. Qafzeh 1 and 2 are firmly associated with modern humans, whereas Qafzeh 6 takes an intermediate position and Skhul V is closer to the ‘archaic’ fossils.

Second and fourth dimensions of the scaling underline the position of outliers in the comparative sample (Fig.5.21b). Skhul V and La Quina are found opposite and most different in the second dimension of the scaling, whereas Shanidar deviates from the majority of the sample in the fourth dimension. Šal’a is also found relatively distant from other Neanderthals in both dimensions. In sum, this analysis seems to demonstrate that, on the one hand, there is a considerable amount of variation within the Neanderthal sample. On the other hand, Skhul V is deemed an outlier in the second dimension of the scaling. In other words, this fossil possesses some ‘unique’ combination of characteristics that make it different from both modern humans and ‘archaic’ forms. None of the North-East Eurasian fossils in the analysis demonstrate such a profound difference with the majority of the sample.

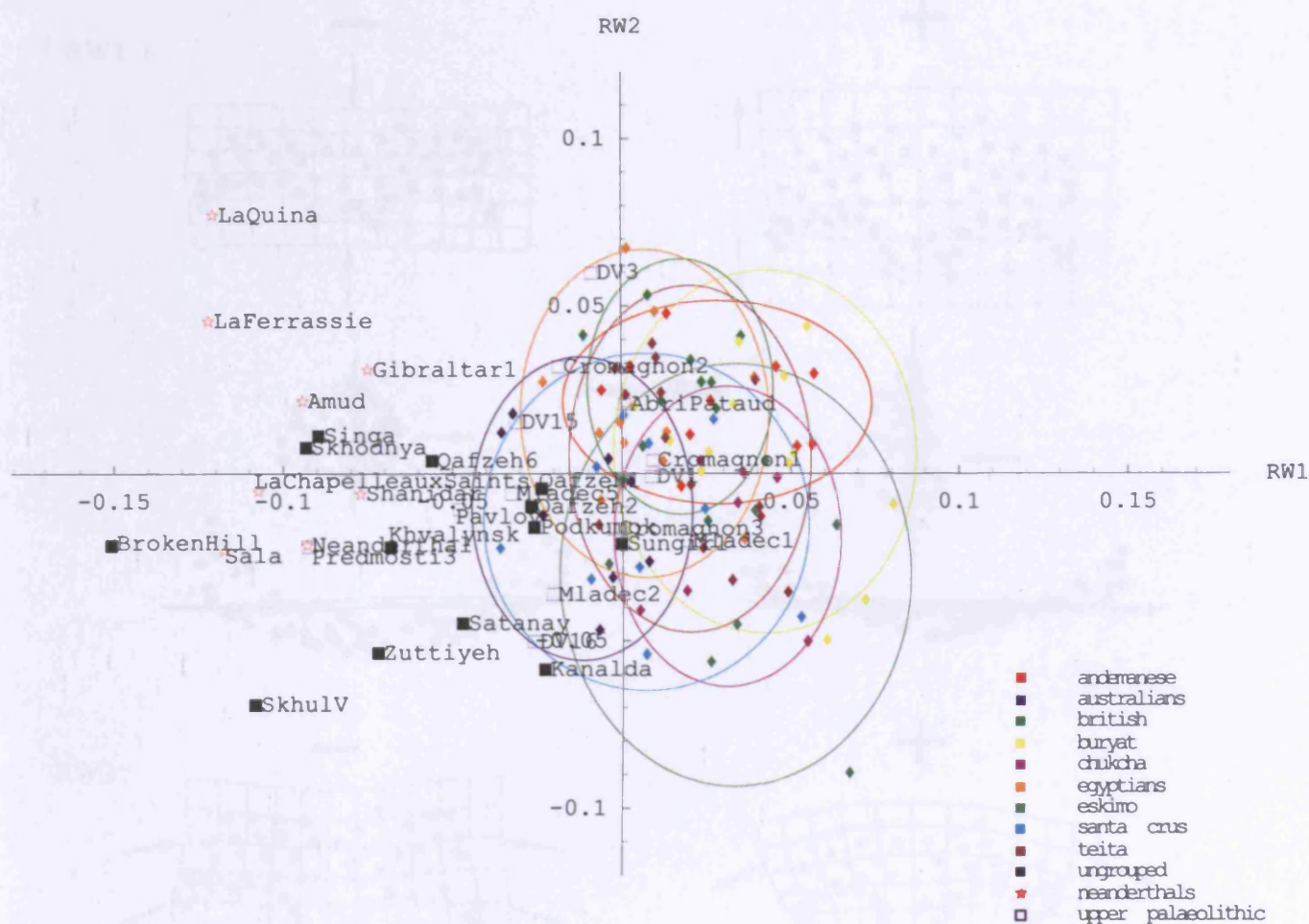
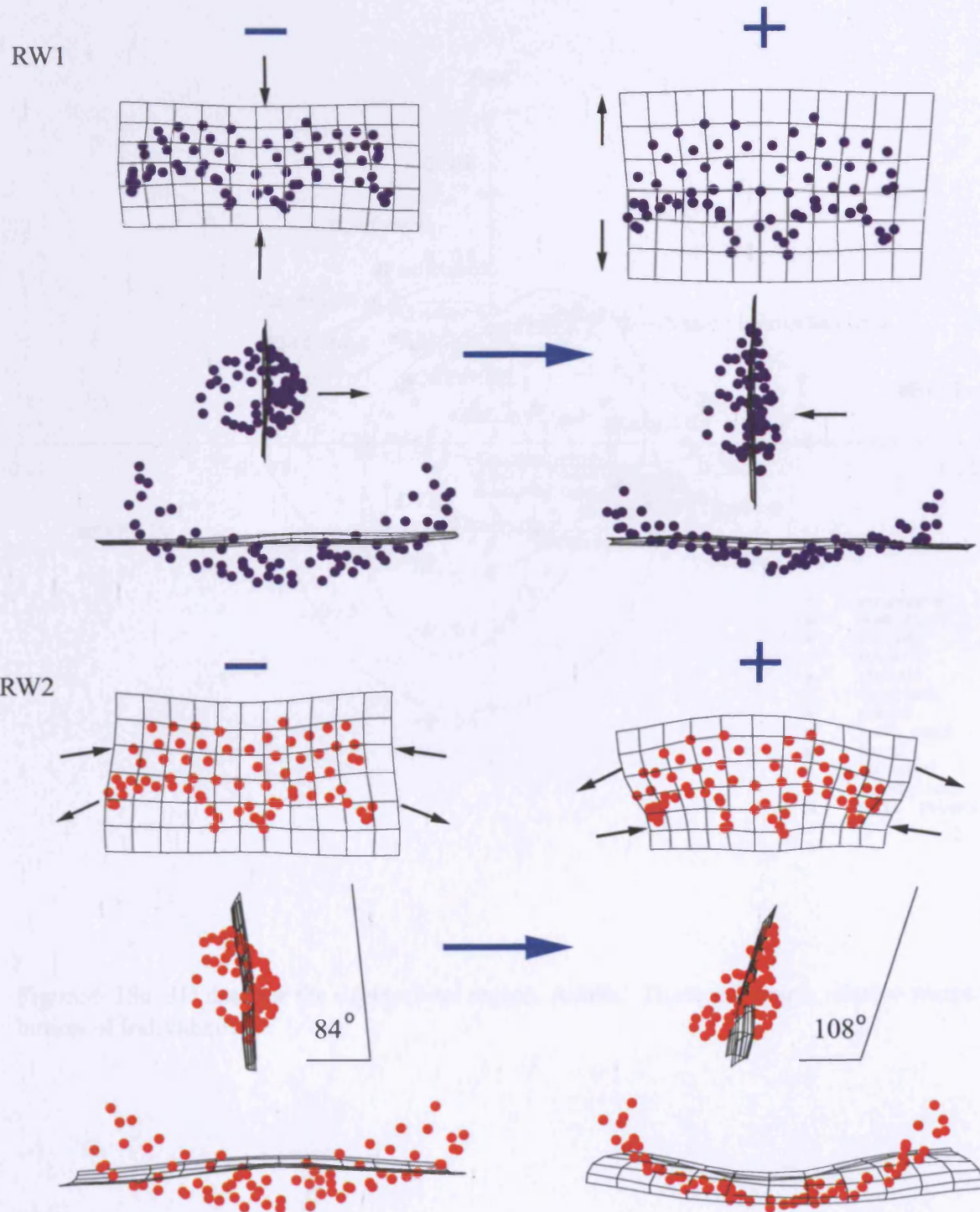


Figure 5.17a. 3D data for the supraorbital region. Adults. First and second relative warps: distribution of individuals.



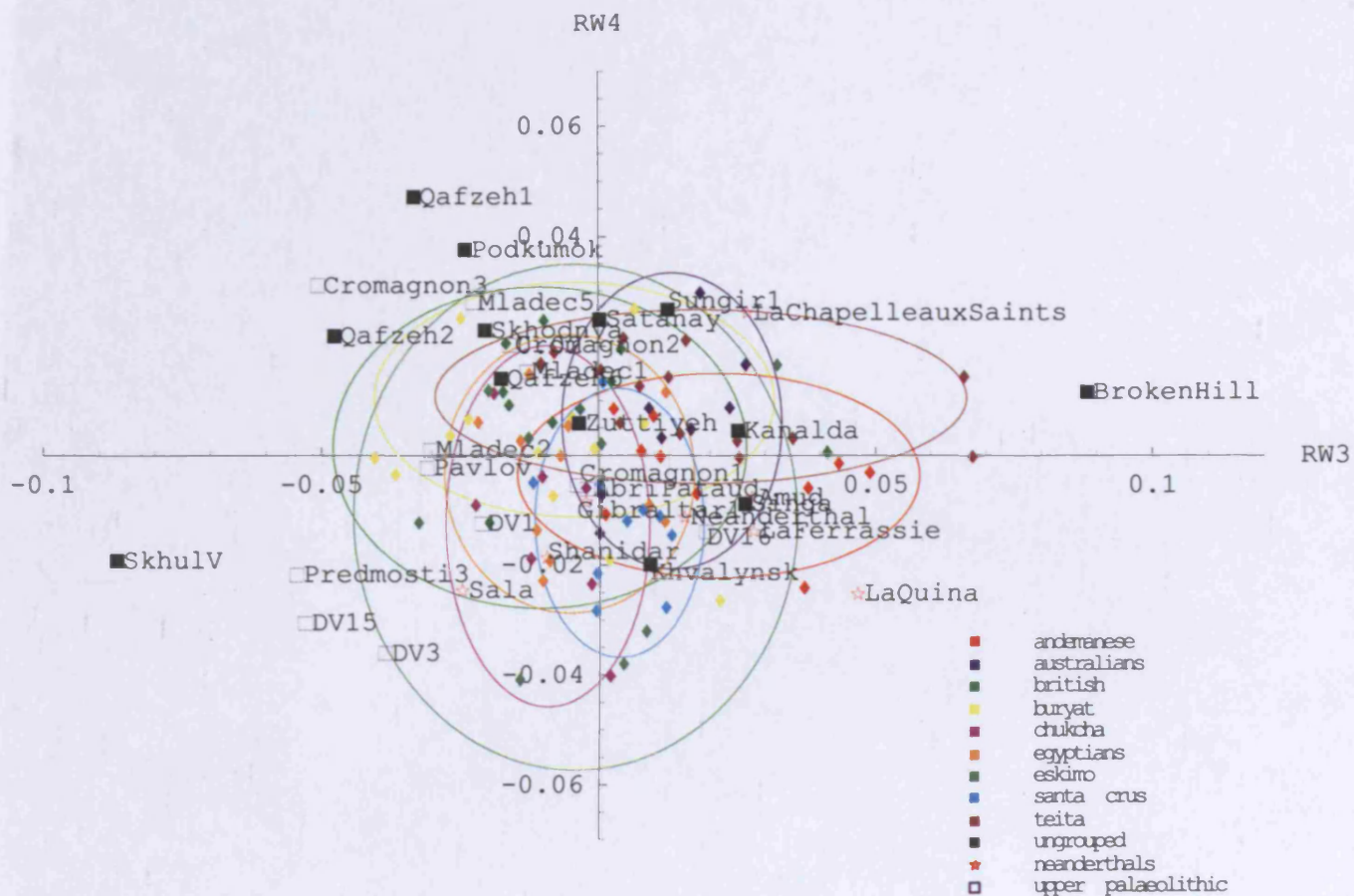
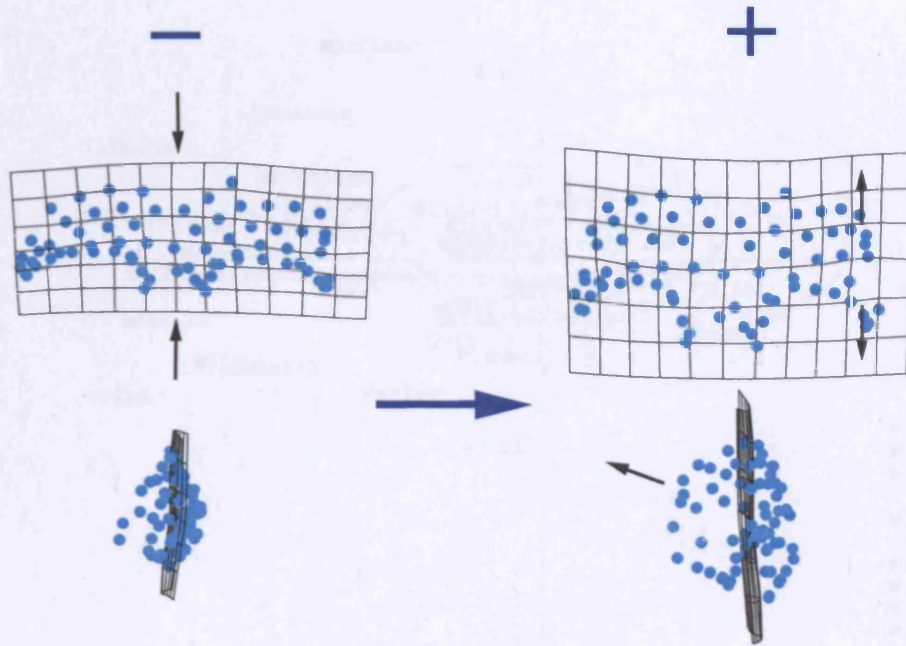


Figure 5.18a. 3D data for the supraorbital region. Adults. Third and fourth relative warps: distribution of individuals.

RW3



RW4

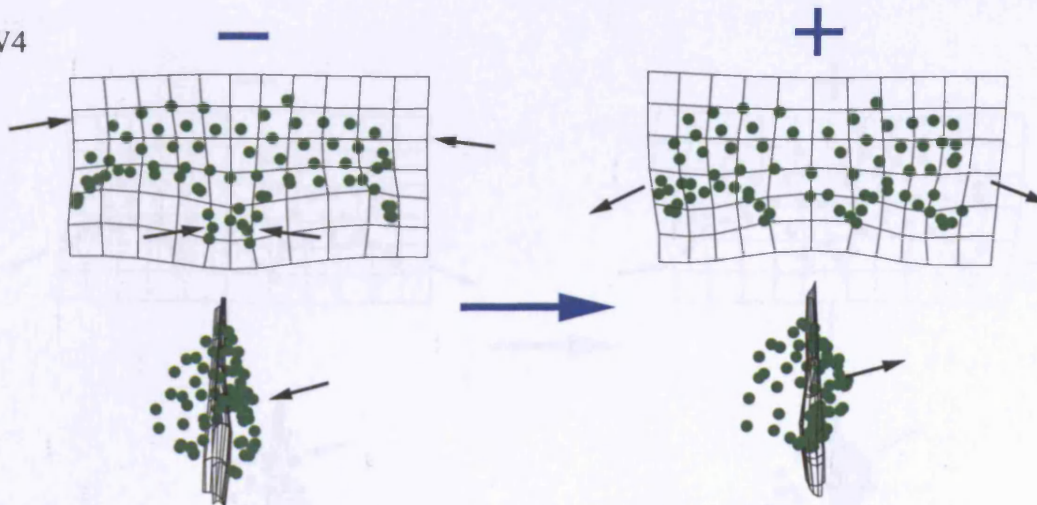


Figure 5.18b. 3D data for the supraorbital region. Adults. Third and fourth relative warps: morphological trends described. TPS transformation of the consensus shape grid towards the target of a shape three standard deviations away from the consensus.

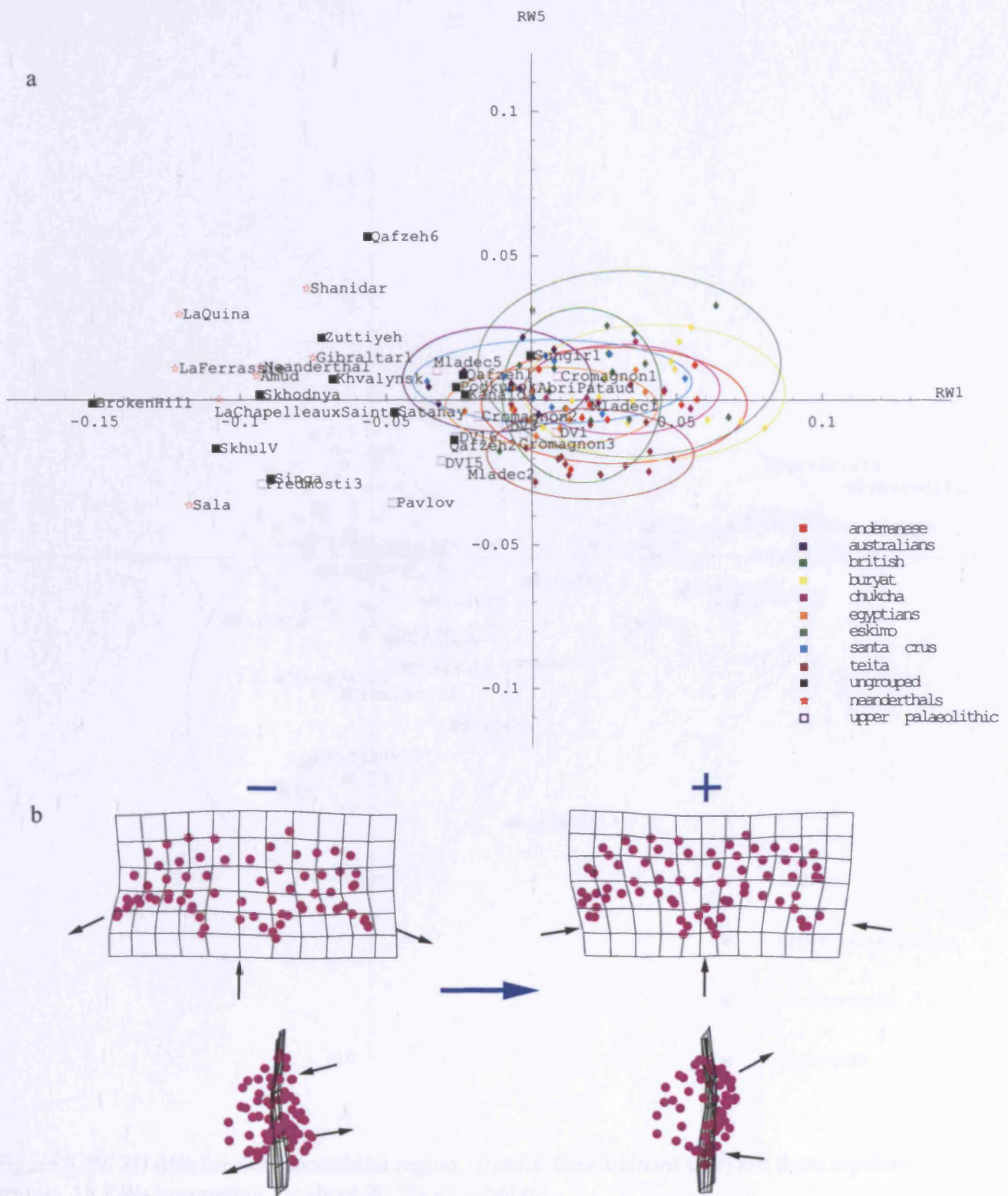


Figure 5.19. 3D data for the supraorbital region. Adults. First and fifth relative warps: a) individual distribution; b) morphological trend described by RW5.

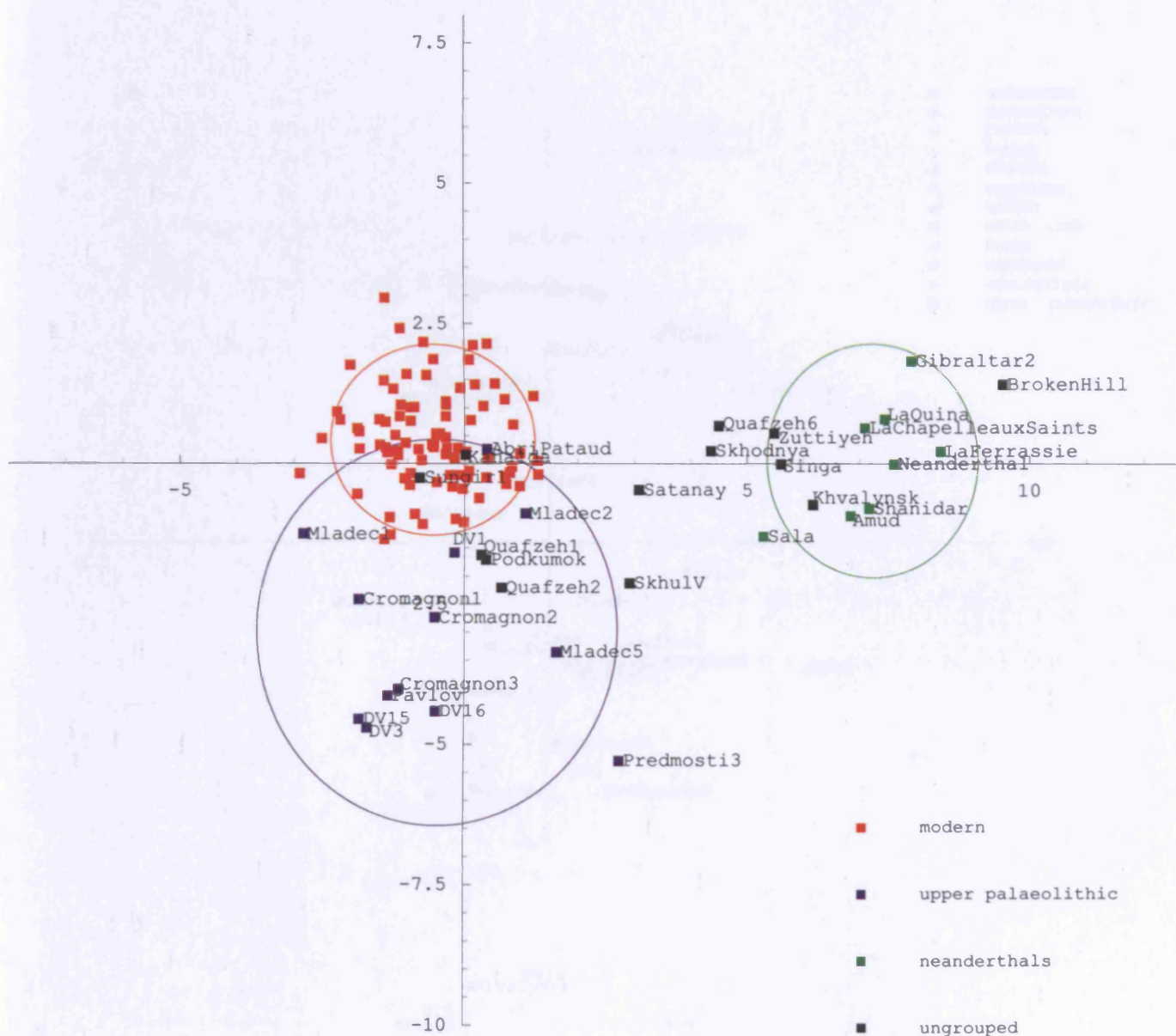


Figure 5.20. 3D data for the supraorbital region. Adults. Discriminant analysis: three a-priori groups, 18 RWs accounting for about 90.3% of variation.

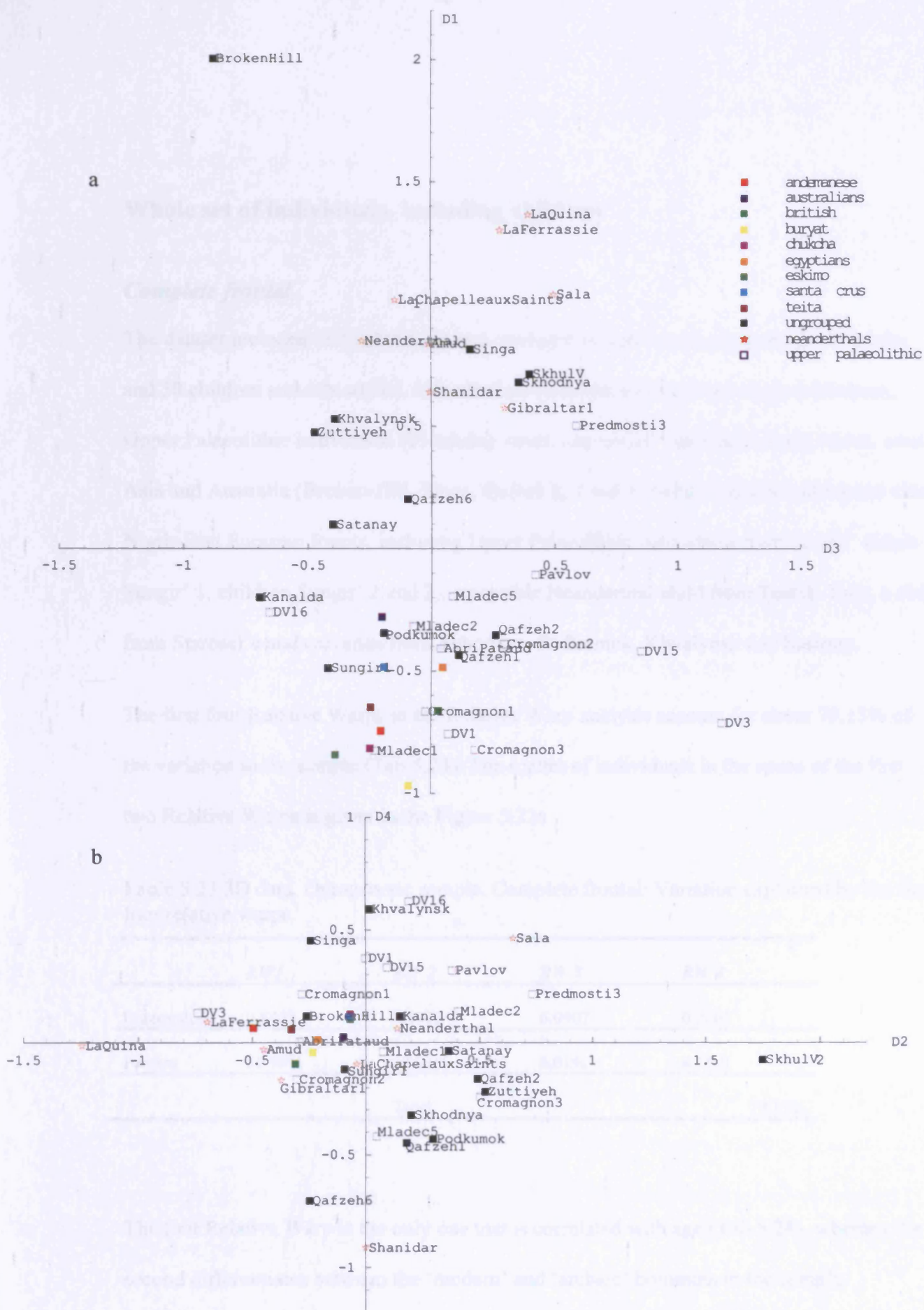


Figure 5.21. 3D data for the supraorbital region. Adults. Results of the Multidimensional scaling: a) first and third dimensions; b) second and fourth dimensions.

Whole set of individuals, including children

Complete frontal

The dataset included 162 individuals and consisted of nine recent populations (91 adults and 30 children and sub-adults), Neanderthals (8 adults and 4 sub-adults and children), Upper Palaeolithic individuals (13 adults), seven ungrouped individuals from Africa, west Asia and Australia (Broken-Hill, Singa, Qafzeh 1, 2 and 6, Skhul V and Kanalda) and nine North-East Eurasian fossils, including Upper Palaeolithic individuals from Sungir' (adult-Sungir' 1, children Sungir' 2 and 3), a possible Neanderthal child from Teshik-Task, a child from Starosel'e and calvarias from Skhodnya, Podkumok, Khvalynsk and Satanay.

The first four Relative Warps in the Relative Warp analysis account for about 79.15% of the variation in the sample (Tab.5.23). The scatter of individuals in the space of the first two Relative Warps is given in the Figure 5.22a

Table 5.23 3D data. Ontogenetic sample. Complete frontal: Variation explained by the first four relative warps.

	<i>RW1</i>	<i>RW 2</i>	<i>RW 3</i>	<i>RW 4</i>
Eigenvalues	0.8458	0.1928	0.0907	0.0665
Percent	55.98%	12.76%	6.01%	4.4%0
Total				79.15%

The first Relative Warp is the only one that is correlated with age (Tab.5.24), whereas the second differentiates between the 'modern' and 'archaic' hominins in the sample

(Fig.5.22a). Therefore, Figure 5.22a may be taken as representative of the group ontogenetic trends in the data.

Table 5.24 3D data. Ontogenetic sample. Complete frontal: Correlation of the principal components with age in the analysis.

	<i>Spearman Rank correlation</i>	<i>t-test of significance at 0.01% level</i>	<i>Kendal Rank correlation</i>	<i>t-test of significance at 0.01% level</i>
PC1	-0.65	True	-0.53	True
PC2	0.12	False	0.09	False
PC3	0.02	False	0.16	False
PC4	0.11	False	0.08	False

From the positive to negative pole, the first RW describes the transformation of the highly curved, “bulging” frontal in children, which is also characterised by a relatively wide posterior aspect of the squama and narrower temporal and supraorbital areas to a flat frontal with relatively narrow posterior aspect of the squama and laterally expanded supraorbital portion in adults (Fig.5.22b). RW2 describes differences between relatively flat frontal bones with highly expanded supraorbital relief in Neanderthals and other ‘archaic’ forms such as Broken Hill and considerably more curved frontal bones in modern humans, who also lack any supraorbital relief but show a laterally expanded middle portion of the frontal (Fig.5.22b).

According to the present results, Neanderthals have a different trajectory of the frontal bone growth from one in modern humans (Fig.5.22a). The youngest Neanderthals (Engis, Gibraltar 2 and Pech de l’Aze) are already different from the recent modern humans in the space of the first and second Relative Warps. Then, the Neanderthal growth trajectory diverges even more towards the adult shapes of the frontal so that the adult shapes differ to

a larger degree than the juvenile ones. This picture agrees with the conclusion by Ponce de León and Zollikofer (2001) on the presence of morphological differences between modern humans and Neanderthals as early as the tooth development stage two (about two years of age) but is different in establishing divergence of the growth trend in Neanderthals respectively recent modern humans. In their work, Ponce de Leon and Zollikofer (2001) detected postnatal parallelism of the development patterns in Neanderthals and modern humans.

It has been expected that immature North-East Eurasian fossils would associate with individuals of the appropriate age and, as the case may be, taxonomic status. According to the present result, Teshik-Tash is placed along the Neanderthal growth trajectory away from the recent modern humans space of the first two relative warps (Fig.5.22a) thus corroborating its present classification. However, the estimated age of Teshik-Tash is about nine years, whereas other juvenile Neanderthals in the analysis (for the exception of Le Moustier) are under 4 years of age. The box plots of the first two components for the complete frontal bone data (Fig.5.23) give a better view of the Teshik-Tash association with these very young Neanderthals along RW1 and its position between Neanderthals and adult Upper Palaeolithic modern humans along RW2 thus pointing out its differences from the West European representatives of the Neanderthal species. The frontal bone of the Starosel's child, to the contrary, falls within the modern human distribution along the second RW, highlighting its modern morphology. Sungir' 2 and 3 are placed within the distribution of recent modern human children.

Unfortunately, the present sample does not have any other Upper Palaeolithic children apart from the individuals from Sungir', and also has no immature individuals from the abundant

west Asian collection of fossils. It is therefore impossible to establish any ontogenetic trajectories apart from recent modern human and Neanderthal ones. For instance, it is not clear whether Upper Palaeolithic modern humans might have differed from recent humans in their ontogeny. It is also not clear if the ontogenetic trajectory of the west Asian early anatomically modern humans would overlap with the ontogenetic trajectory of Neanderthals as do some of the adult individuals (i.e. Skhul V and Qafzeh 6). Addition of the immature individuals from these populations may affect the conclusion on the association of, for example, Teshik-Tash with Neanderthals.

An opinion on the possible young age of Satanay, expressed elsewhere (Kharitonov, personal communication; Romanova and Kharitonov, 1989) is not supported by the present results. Satanay strongly deviates towards the 'adult' negative pole of RW1. Among other North-East Eurasian fossils, Khvalynsk and Skhodnya are placed very close to each other among adult individuals of 'intermediate' morphology. In other words, morphologically they are positioned between Neanderthals and recent modern humans in close proximity to Mladeč 2, Qafzeh 2, Cro-Magnon 2 and Zuttiyeh. Podkumok and Sungir' 1 are placed among the recent adult individuals.

Third and fourth relative warps cumulatively account for about 10.4% of variation in the sample. None of these components are significantly correlated with age (Tab.5.24). Recent modern populations, Neanderthals and Upper Palaeolithic overlap in the space of RW3 and RW4 (Fig.5.24a). However, as in the analysis of adult individuals, the majority of the Upper Palaeolithic individuals differ along the third or third and fourth relative warps from the recent modern sample, whereas Skhodnya, Khvalynsk and Skhul V demonstrate high differentiation from the rest of the sample along RW4.

The third relative warp accounts for the differences between relatively narrow and bulging frontal as is characteristic for Moravian fossils such as Pavlov, DV3, DV16 as well as, to a lesser extent, a number of other Upper Palaeolithic individuals and flat and relatively wide frontals as in Neanderthals such as Gibraltar 1 and La Chapelle aux Saints (Fig.5.24b). The fourth relative warp mostly differentiates between forms with a relatively narrower posterior aspect of the squama that have laterally expanded medial and anterior portions and bulging forehead and forms with a narrower temporal region, long and ‘sloping’ sides of the coronal suture with posteriorly located bregma, flat forehead and slightly better developed browridges. There is also a difference in the relative inclination of the frontal, with it being more vertical at the negative pole of the component (Fig.5.24b).

In this space, Teshik-Tash is closely related to such Neanderthal forms as Gibraltar 2 and Shanidar. Šal’a is also very close to Teshik-Tash along RW3 (Fig.5.25a). However, given that the positions of all these forms overlap with recent modern human variation, it is difficult to assign any diagnostic value to the listed features.

As it is mentioned above, Skhodnya and Khvalynsk are very different from the majority of the sample along RW4, which is clearly seen in the one-dimensional representation of the Relative Warps in Figure 5.25b. Podkumok, however, is better associated with the Upper Palaeolithic individuals (Fig.5.24a and 4.25b). Starosel’e deviates towards the Moravian Upper Palaeolithic fossils along RW3 being different from Neanderthals with wide and flat frontal bone on one hand and forms such as Skhul V, Skhodnya and Khvalynsk on the other (Fig.5.24a). Sungir’ 1, 2 and 3 are placed relatively close together well within the recent modern human distribution showing very little association with the distinctive Upper

Palaeolithic forms along RW3. Satanay is also placed within the recent modern human distribution in proximity to Šal'a, Qafzeh 6 and Mladeč 2.

The overview of each Relative Warp separately provided by Box plots shows that groups do not differ significantly along RW1 (Fig 4.23a), whereas Neanderthals significantly differ from Upper Palaeolithic and recent groups along RW2 (Fig 4.23b). At the close inspection of the second Relative Warp one can see that Teshik-Tash association with the Neanderthals is not absolutely unquestionable. Along this warp it is positioned just outside the Neanderthal span of variation at the overlap with the adult Upper Palaeolithic modern humans. This result is may have been brought about by the bias of the sub-adult Neanderthal sample towards the West European Neanderthals (Engis, Pech de l'Aze and Le Moustier). For example, it has been shown in the analysis of the inter-landmark distances that Teshik-Tash differs from young Neanderthals by its flatter upper face. This analysis has also revealed that the combination of the 'archaic' features of the frontal is also expressed to a lesser degree in Teshik-Tash than in the Neanderthal children but more than in such Upper Palaeolithic adults as Předmostí 3 and Mladeč 5.

Some differentiation of the Upper Palaeolithic group is described by the third Relative warp (Fig.5.25a), whereas the fourth relative warp best differentiates between Neanderthals and Upper Palaeolithic modern humans (Fig.5.25b). The recent populations, however, demonstrate a large variation span along the fourth relative warp to the extent of encompassing variation in both Upper Palaeolithic and Neanderthal groups. Skhul V, Skhodnya and, to a lesser extent, Khvalynsk fall outside the variation in the recent modern human populations.

In sum, the results of this analysis argue that Teshik-Tash can be placed along the growth trajectory of the Neanderthals. However, it has lesser degree of the expression of the 'archaic' suite of features of the frontal than the juveniles of the West European Neanderthals. The Starosel's child has demonstrated lack of association with the 'archaic' hominins in the sample. The Sungir' individuals fit well within the recent modern human distribution with Sungir' 2 and 3 taking appropriate positions among recent children. Moreover, Sungir' individuals show relative similarity to each other in some aspects of morphology (as, for example, described by RW2 and RW4). There is no evidence for association of Satanay with immature forms. In respect of the other adult North-East Eurasian individuals, the results of the present analysis agree with conclusions made on the basis of the analysis of adults. Thus, Podkumok shows a good association with modern humans deviating toward the Upper Palaeolithic forms in finer aspects of morphological variation as described by RW3 and RW4. Skhodnya and Khvalynsk are very similar in the space of the first two relative warps that account for 68.74% of variation. These two calvarias are interesting due to their 'intermediate' position between Neanderthals and recent modern humans in the space of the first two relative warps. As in the analysis of the adult individuals, they demonstrate aspects of morphology that make them similar to Skhul V in their relatively narrow temporal region, flatter frontal, raised supraorbital relief coupled with the longer and sloping sides of the coronal suture.

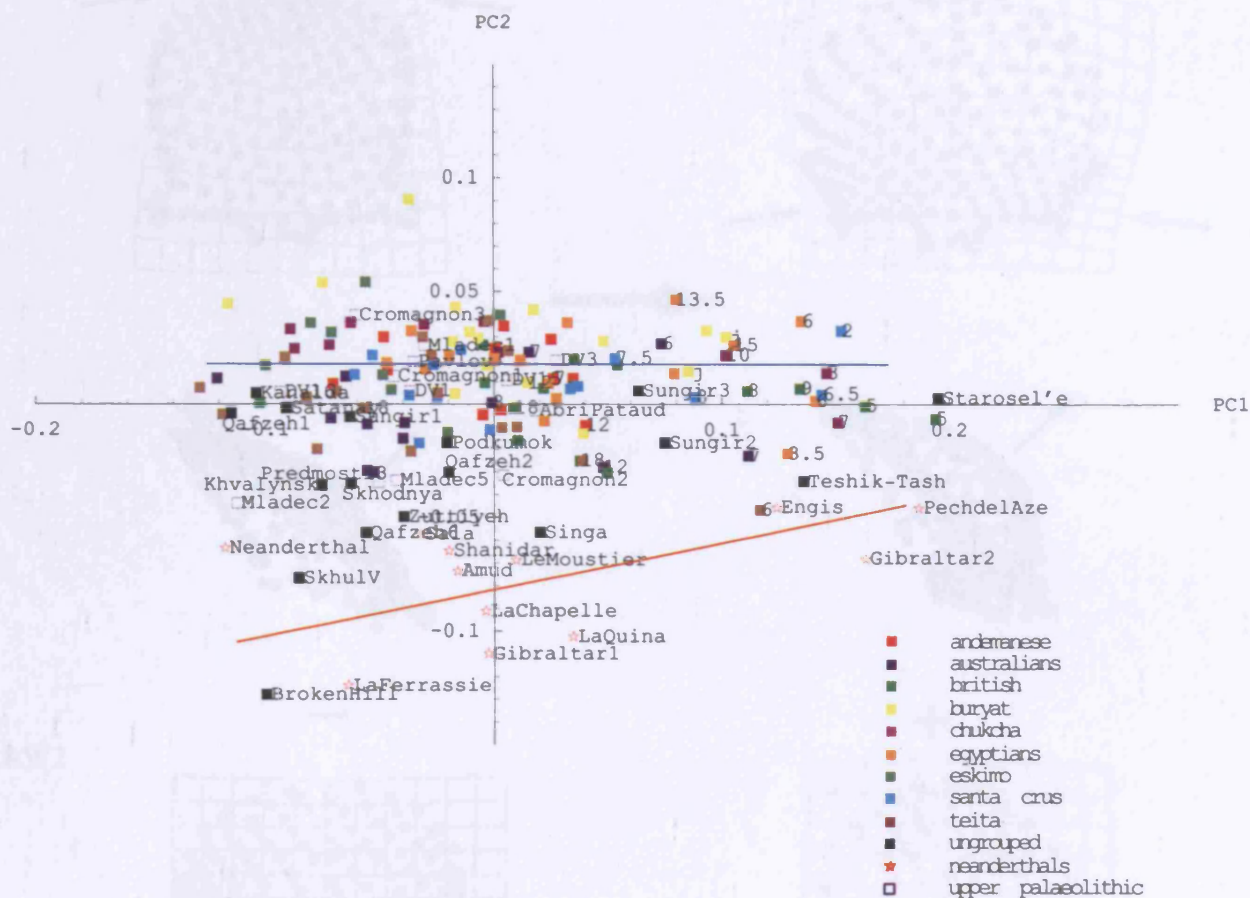


Figure 5.22a. 3D data for the complete frontal bone. Ontogenetic dataset. Distribution of individuals in the space of the first and second relative warps. Recent sub-adults are additionally marked by their age. Blue and red lines highlight modern human and Neanderthal ontogenetic trajectories respectively.

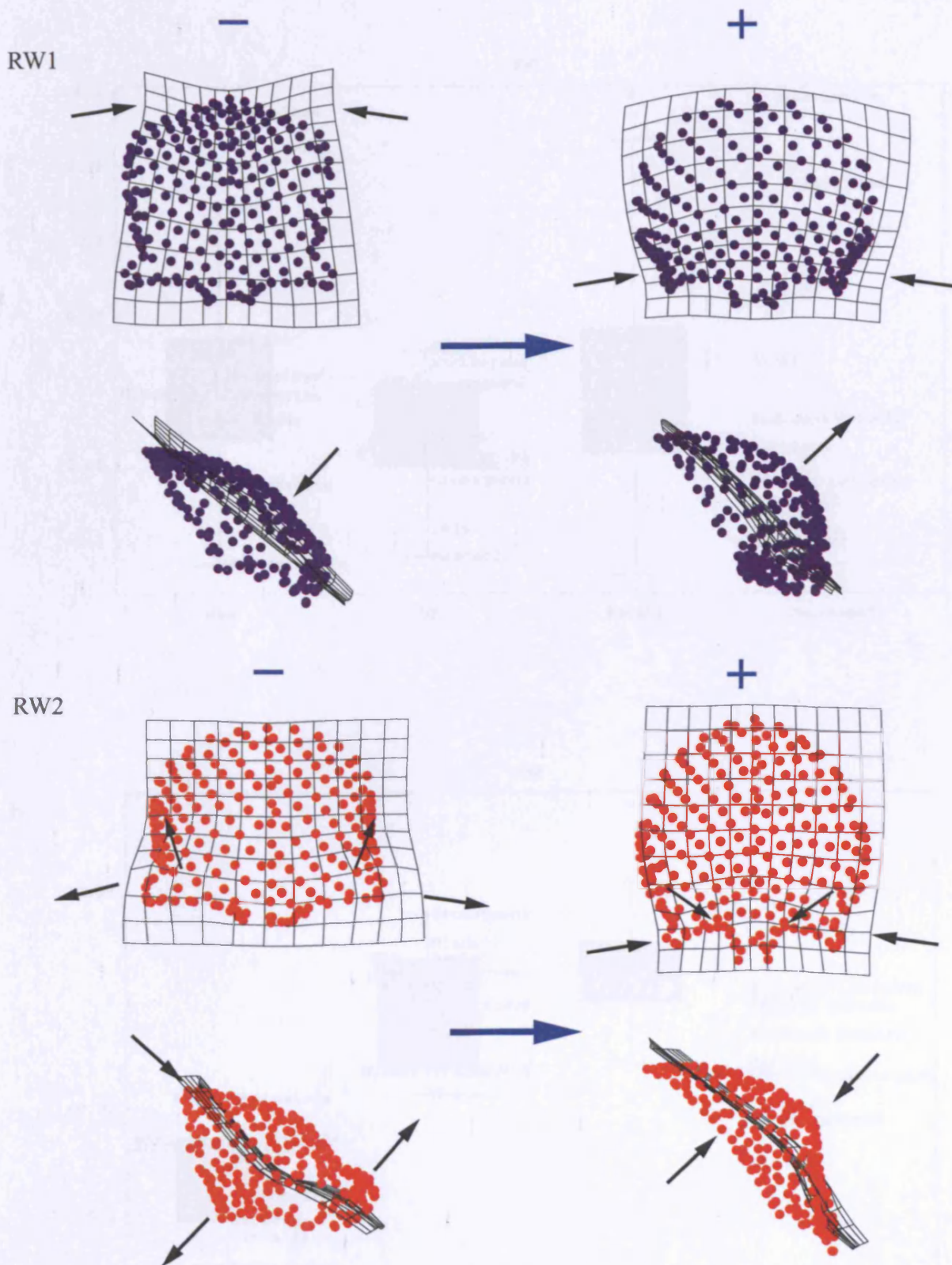


Figure 5.22b. 3D data for the complete frontal bone. Ontogenetic dataset. Morphological trends described by the first and second relative warps. TPS transformation of the consensus shape grid towards the target of a shape three standard deviations away from the consensus.

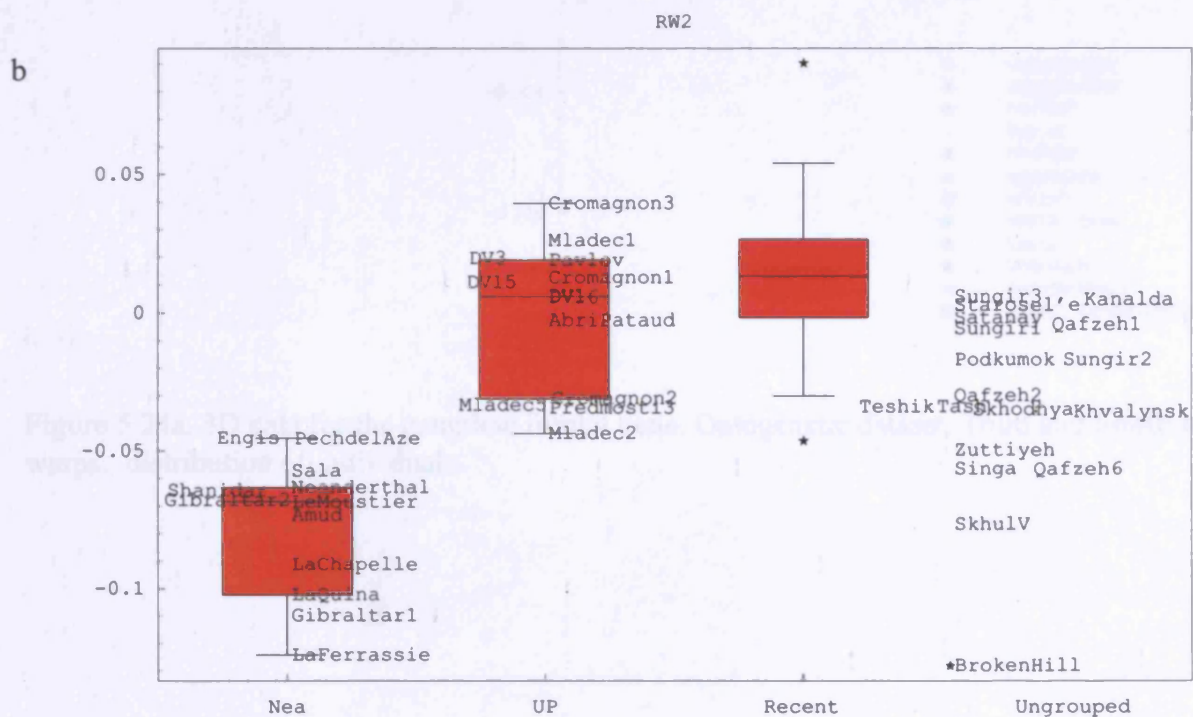
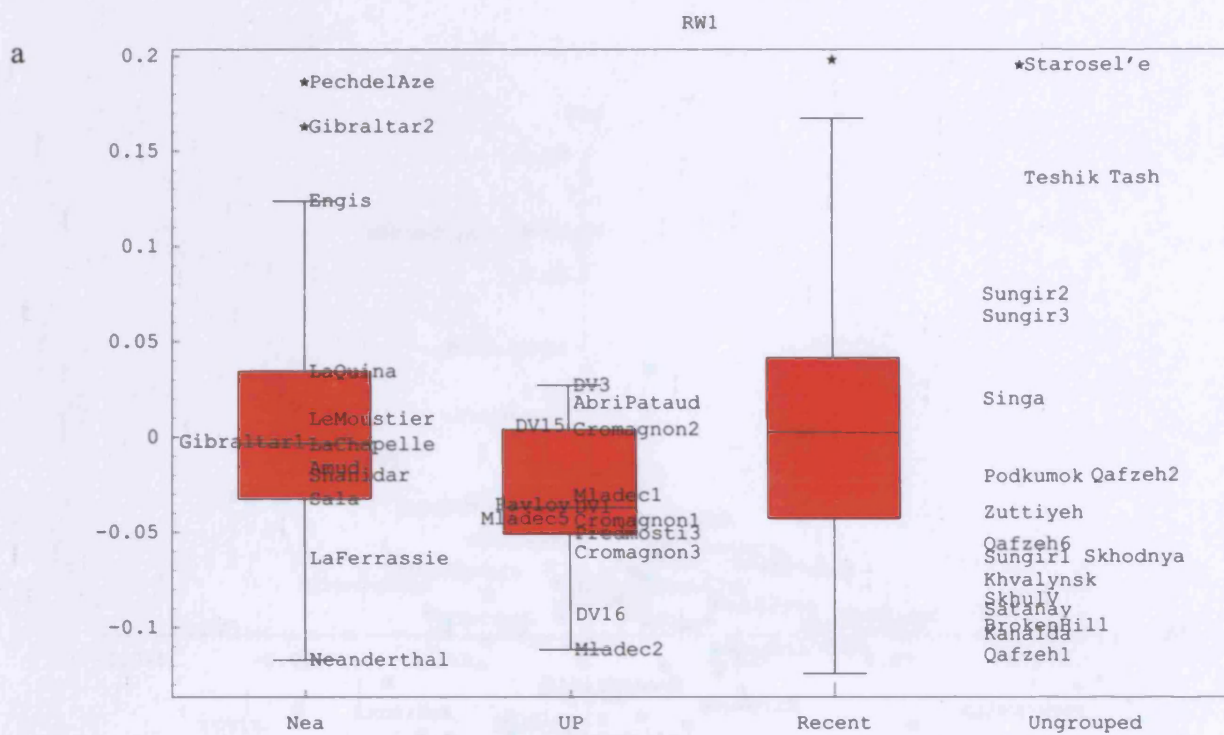


Figure 5.23. 3D data for the complete frontal bone. Ontogenetic dataset. Box plots for : a) RW1; b) RW2. See explanation for the Figure 4.5.

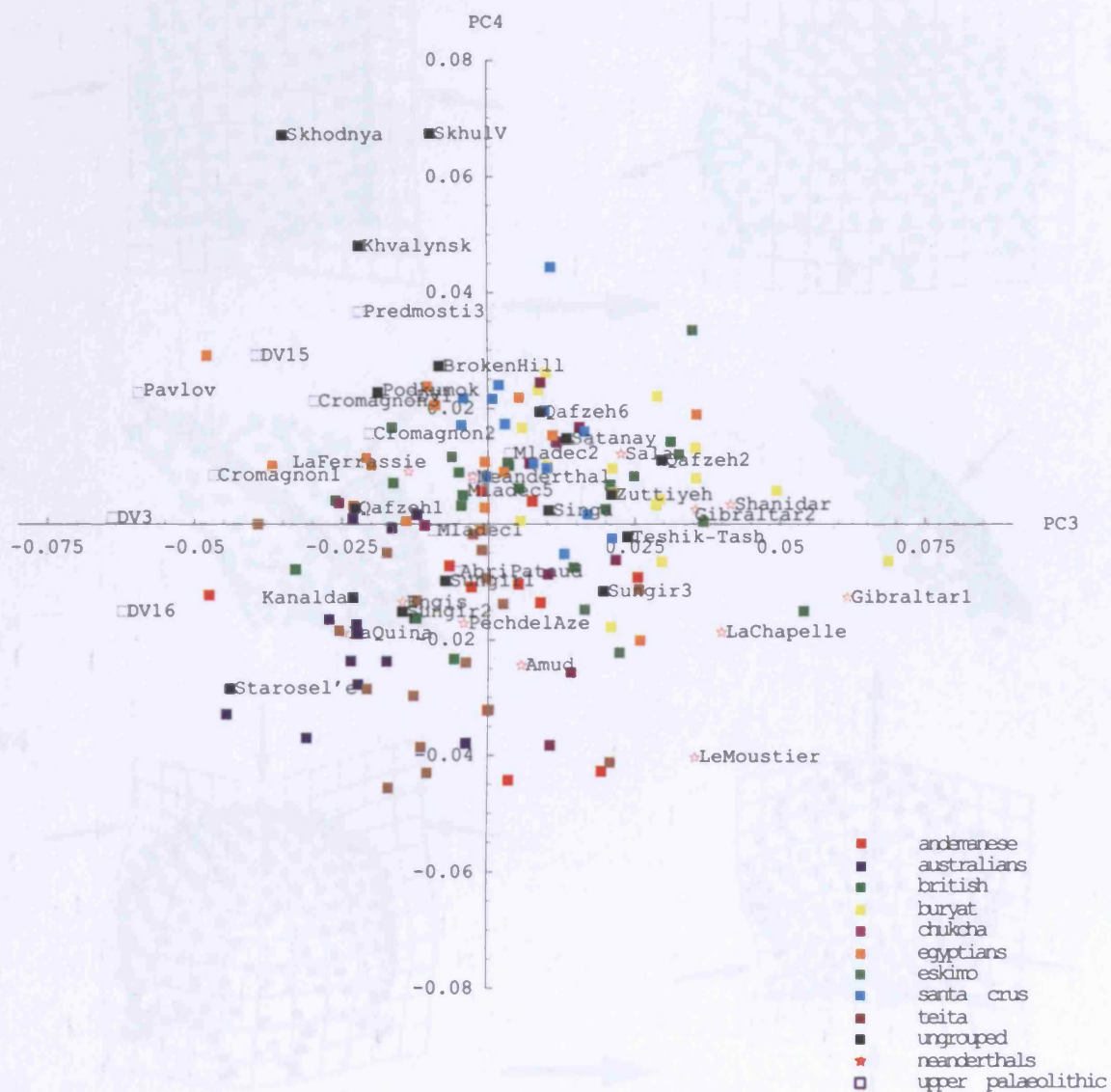
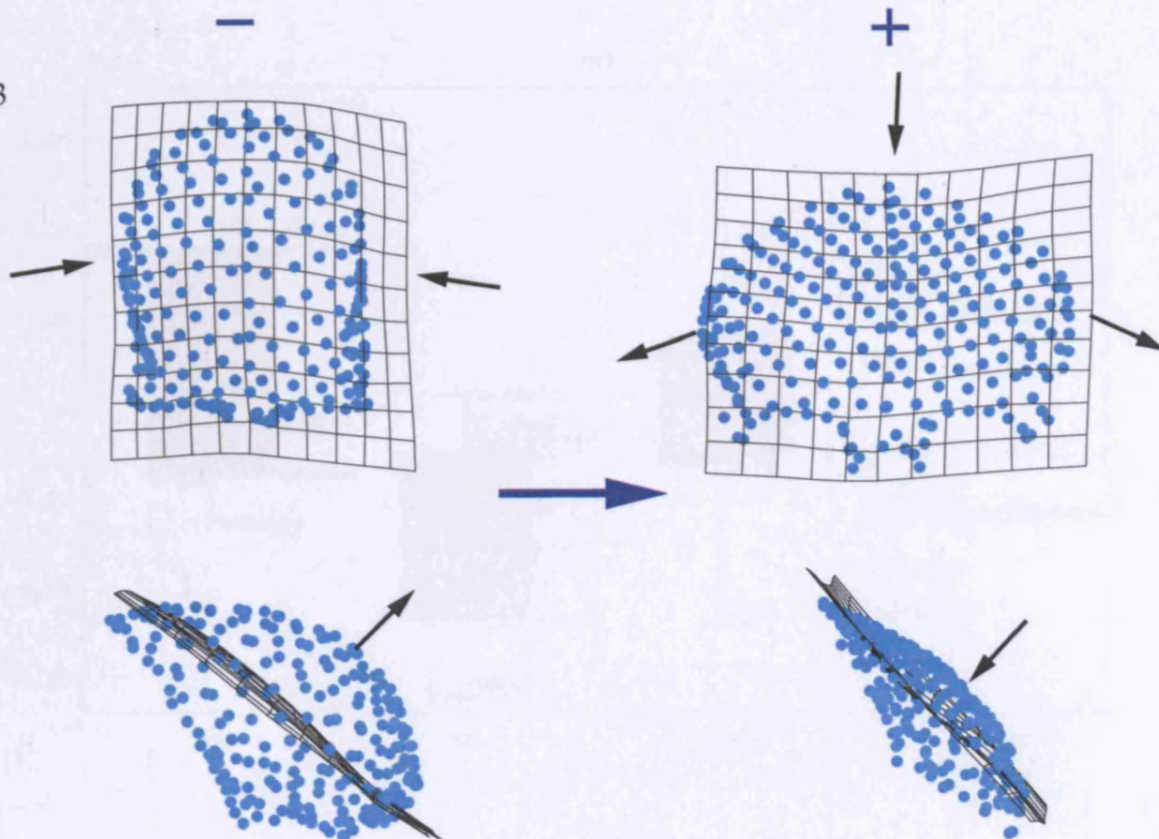


Figure 5.24a. 3D data for the complete frontal bone. Ontogenetic dataset. Third and fourth relative warps: distribution of individuals.

RW3



RW4

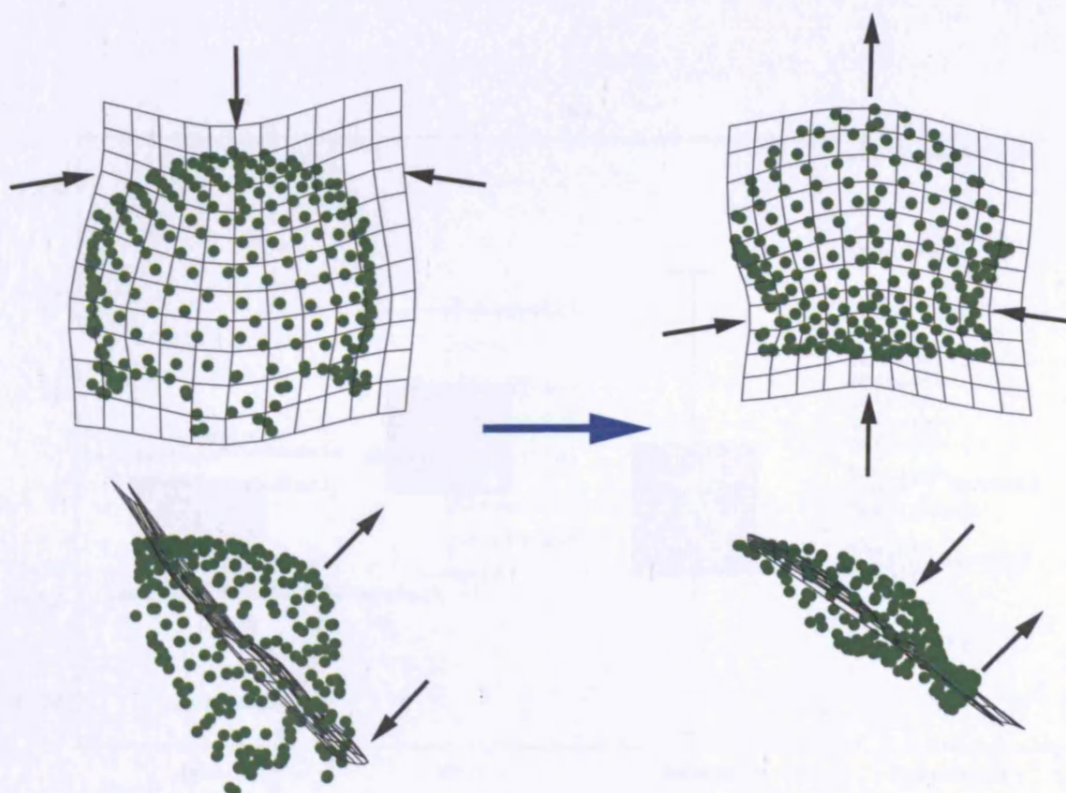


Figure 5.24b. Analysis of all individuals, complete frontal bone: morphological trend described by the third and fourth relative warps. TPS transformation of the consensus shape grid towards the target of a shape three standard deviations away from the consensus.

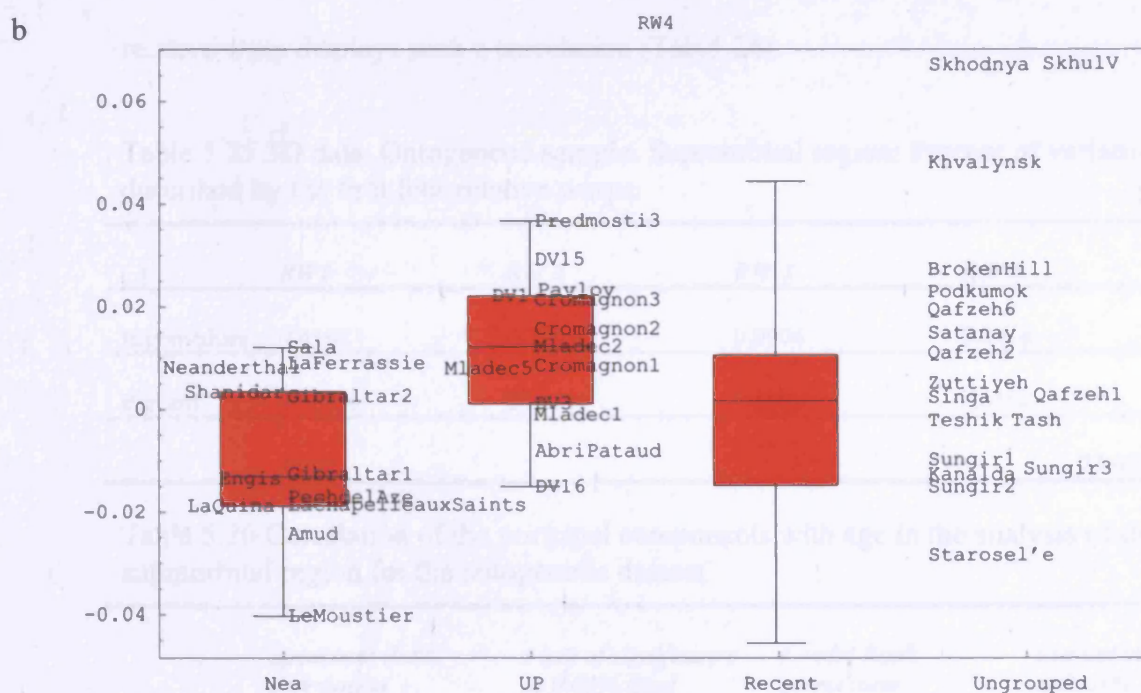
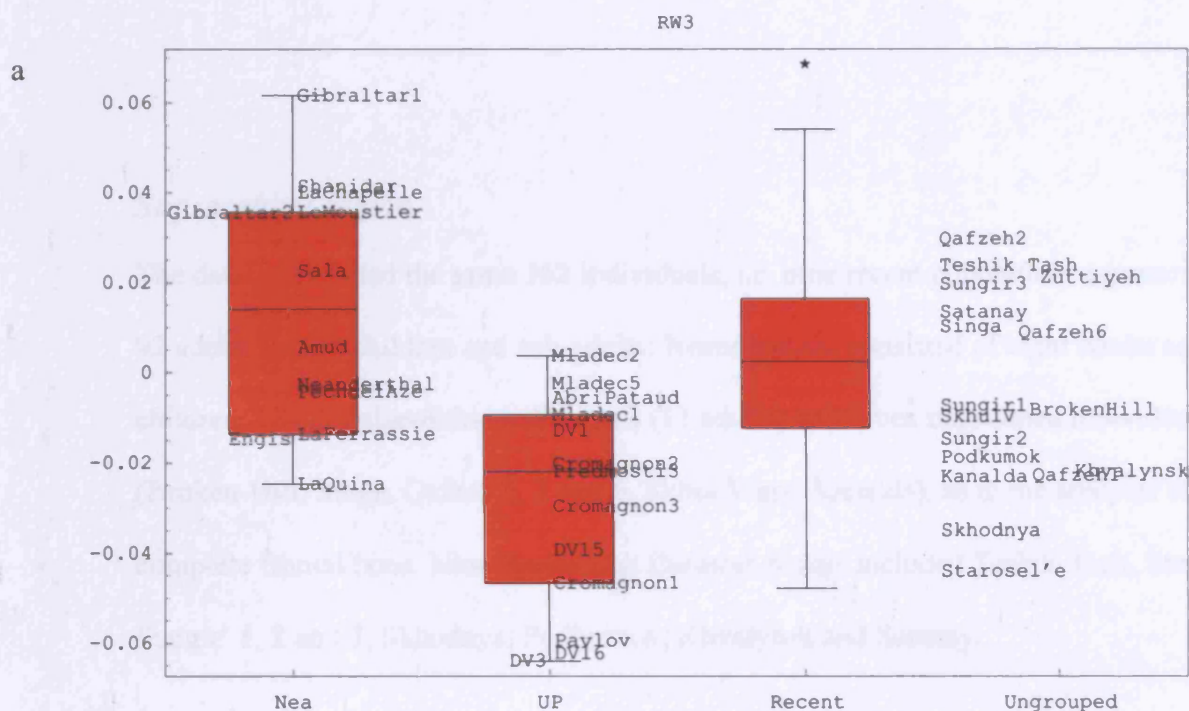


Figure 5.25. 3D data for the complete frontal bone. Ontogenetic dataset. Box plots for : a) RW3; b) RW4. See explanation for the Figure 4.5.

Supraorbital region

The dataset included the same 162 individuals, i.e. nine recent populations represented by 92 adults and 30 children and sub-adults; Neanderthals, consisted of eight adults and four children; Upper Palaeolithic individuals (13 adults) and seven ungrouped individuals (Broken-Hill, Singa, Qafzeh 1, 2 and 6, Skhul V and Kanalda), as in the analysis of the complete frontal bone. Nine North-East Eurasian fossils included Teshik-Tash, Starosel'e, Sungir' 1, 2 and 3, Skhodnya, Podkumok, Khvalynsk and Satanay.

The first four relative warps in the analysis account for 73.01% of variation in the sample, with the largest part of the variation summarised by the first two relative warps (61.54%) (Table 5.25). RW1 has a significant negative correlation with age whereas none other relative warp displays such a correlation (Tab.5.26).

Table 5.25 3D data. Ontogenetic sample. Supraorbital region: Percent of variation described by the first four relative warps.

	<i>RW1</i>	<i>RW 2</i>	<i>RW 3</i>	<i>RW 4</i>
Eigenvalues	0.4198	0.2874	0.0906	0.0416
Percent	36.53%	25.01%	7.88%	3.61%
Total				73.01%

Table 5.26 Correlation of the principal components with age in the analysis of the supraorbital region for the ontogenetic dataset

	<i>Spearman Rank correlation</i>	<i>t-test of significance at 0.01% level</i>	<i>Kendal Rank correlation</i>	<i>t-test of significance at 0.01% level</i>
PC1	-0.66	True	-0.54	True
PC2	-0.11	False	-0.08	False

PC3	0.04	False	0.03	False
PC4	0.07	False	0.05	False

Given its correlation with age, RW1 may be treated as one that represents an ontogenetic vector in the data. At the same time, RW2 provides for discrimination between modern and archaic individuals (Fig.5.26a). From the negative to the positive values, RW1 describes transformation of the adult shape of supraorbital region into the juvenile one (Fig.5.26b). The supraorbital region in children is described as having inward superior-inferior inclination in the sagittal view, relatively small and rounded orbits, compared to which the breadth across the frontotemporale appears much wider coupled with the relatively higher position of glabella. In the coronal projection, the almost complete absence of projection in either superciliary or supraorbital arches is expressed as the equiplanar position of the supraorbital rims and the areas above them. In adults, the supraorbital region has forward inclination (running superior-inferiorly in the sagittal projection) and relatively narrower breadth across frontotemporale in comparison with the transverse diameter across the supraorbital region that translates to the lateral expansion of the supraorbital margins and relatively larger orbits. The narrowing of the diameter across the frontotemporale (or a smaller Minimum Frontal Breadth) is partly achieved by the relative narrowing of the supraglabellar area that highlights the lateral expansion of the orbits during ontogeny. In the coronal view, one can observe that supraorbital rims are no longer positioned in the same plane as areas above them suggesting some degree of development of the supraorbital relief.

The Box plot representation of the RW1 on Figure 5.27a shows that Upper Palaeolithic modern humans are quite similar to the recent modern humans, whereas Neanderthals have

slightly different pattern of distribution along this relative warp where median of adult Neanderthals corresponds with the upper 25% distribution of the modern ontogenetic dataset, i.e. with relatively young individuals.

RW2 differentiates Neanderthals and other 'archaic' fossils in the sample from the modern humans (Fig.5.26a and 5.27b). Figure 5.26b shows that the 'archaic' shape is characterised by the relative cranio-caudal narrowing and high anterior projection of the area, with particular emphasis on the anterior position of the glabella in the horizontal plane and noticeable expansion of the supraorbital trigonae so that a merged, uniformly rounded and projecting supraorbital torus is formed. There is just a slight deepening of the superior boundary of the TPS grid in the glabella region that may account for the representation of the 'double arching' supraorbital torus in Neanderthal individuals within the sample. The ultimately 'modern' type of the supraorbital region is relatively tall and flat. There is a noticeable narrowing of the mid-line of the area that accounts for the lack of any expansive development of the supraorbital arches and very short and flat, if any, superciliary arches at the most positive values of the RW2 vector. Glabella still takes an anterior position relative to the areas lateral to it. In the coronal projection, supraorbital margins form almost straight lines to the lateral of glabella. Neanderthals, Upper Palaeolithic modern humans and recent modern humans differentiate well along the second component (Fig 5.26b).

In the space of the first two components (Fig.5.26a), Neanderthals and modern humans form distinctive ontogenetic trajectories that start at the relatively close (but still different) positions of the respective juveniles in the sample. The youngest children in the group of recent human population are aged 2 years of age and the youngest Neanderthal, Pech de

l'Aze, is 2.5 years of age. The trajectories then diverge reaching markedly different adult states as described by RW2.

The majority of the adult Upper Palaeolithic individuals overlap with the recent modern humans. Here, DV3 seems to be placed further towards juveniles than any other Upper Palaeolithic fossil in the sample that may be due to its younger age. However, it may also result from the female sex of the DV3 individual, which is not controlled for in the present analysis.

Some of the Upper Palaeolithic fossils show pronounced differences from other individuals of the same group. For example, Předmostí 3 is associated with adult Neanderthals (Fig.5.26a, Fig.5.27). However, Pavlov, DV16 and Mladeč 5 also deviate towards the 'archaic' group of fossils along RW2 not reaching the morphological state of Předmostí 3. A large range of variation is also shown by the west Asian fossils. Qafzeh 1 and 2 are placed close to each other and are associated with modern humans. Qafzeh 6 has an intermediate position between modern humans and Neanderthals along RW2. Zuttiyeh is deemed to be very similar to Neanderthals. At the same time, Skhul V and Šal'a show equally low scores along RW2 allowing room for speculation on the similarity of the relatively narrow browridges in these two fossils. Broken Hill has the lowest values along RW2 and the most extreme expression of the 'archaic' browridge morphology in the sample. In total, it appears that, although there is good differentiation between Neanderthals and modern humans in the morphology of the supraorbital region, Neanderthals overlap in distribution with other 'archaic' forms in the present analysis to the extent that such fossils as Singa and Předmostí 3 fall within the range of distribution of adult Neanderthals.

Within this framework, the following positions are assumed by the North-East Eurasian fossils in the sample. Starosel'e is better associated with the youngest recent modern children, whereas Teshik-Tash is placed close to the Neanderthal ontogenetic trajectory. Unlike in the shape of the complete frontal, Teshik-Tash overlaps with the Neanderthal distribution along the 'archaic' component (RW2) in the shape of its supraorbital relief (Fig.5.27b). It is, however, slightly 'less Neanderthal' along RW2 than the younger child Gibraltar 2. Further investigation of the ontogeny of the early modern humans may clarify the position of Teshik-Tash in relation to this group.

The children Sungir' 2 and Sungir' 3 fall within the distribution of the immature recent individuals with Sungir' 3 being deemed to have a more 'adult' morphology than Sungir' 2 (Fig.5.26a, Fig.5.27). This is a surprising result given that Sungir' 3 has been previously defined as a girl of 9–10 years of age and Sungir' 2 as a boy of about 12–13 years of age (Zubov, 2000; Mednikova et al., 2000). As expected, Sungir' 1 is associated with the adult recent modern humans in browridge morphology. It scores low negative values along RW1 thus displaying a relatively advanced level of 'adult' combination of features. All other North-East Eurasian fossils in the sample, namely, Podkumok, Satanay, Skhodnya and Khvalynsk associate with adults. Podkumok is closer to modern adults, such as Mladeč 2, Mladeč 5, DV15, Qafzeh 1 and 2. Satanay shows a stronger deviation towards the 'archaic' morphology, whereas Khvalynsk and, in particular, Skhodnya are better associated with the 'archaic' forms.

RW3 and RW4 account for about 11% of the variation cumulatively. Neanderthals, Upper Palaeolithic and ungrouped individuals show great overlap with the recent human variation in the space of RW3 and RW4 (Fig 4.28a). However, there is some structure observable on

the scatter plot of individual scores in the space of RW3 and RW4 . First of all, Neanderthals tend to separate from the Upper Palaeolithic group having mostly positive values along one or both relative warps and flanking recent modern human variation. Upper Palaeolithic individuals, however, tend to assume negative values along RW3 with some of them present as outliers in comparison with the recent human variation in the space of the third and fourth relative warps. For example, Předmostí 3 and DV15 strongly deviate along RW3 towards the narrow browridges as in Skhul V. Mladeč 5 is placed close to Qafzeh 1 along RW4, whereas Cro-Magnon 3 shows relatively low scores along both relative warps.

The morphological trend along RW3 is dominated by the opposition of the narrow browridges in Skhul V and tall and relatively larger browridges in Broken Hill (Fig.5.28b and Fig.5.29a). Among other features characteristic of this opposition are the relatively deeper glabella in Skhul V and a more forwardly placed glabella in Broken Hill as seen in horizontal projection (Fig.5.28b).

RW4 describes a trend between shapes with wider interorbital distances, the respective narrowing of the orbital breadths and deeper position of nasion in contrast with the shapes that have narrower interorbital distances, wider orbits and a relatively more anterior position of nasion (Fig.5.28b). Qafzeh 1 has the most negative scores along this component (Fig.5.28a and Fig.5.29b) showing the extreme case of combination between large interorbital breadth, narrow orbits and deep nasion. The opposite morphological combination is noted for one Chukcha and two Eskimo individuals along RW4 (Fig.5.28a).

Within the above picture, Teshik-Tash, Starosel'e, Satanay, Skhodnya, Sungir' 1, 2 and 3 are placed within the main distribution of individuals thus displaying no extreme

expression of feature combination, as described by RW3 and RW4 (Fig.5.28a). However, Khvalynsk is among the few individuals that score high values along RW4. This fossil displays a combination of relatively narrow interorbital distance, wider orbits and less prominent position of glabella in comparison with the rest of the sample. Shanidar has similar to Khvalynsk scores along both RW3 and RW4, whereas Skhul V is similar to Khvalynsk along RW4. Unlike Khvalynsk, Podkumok and Sungir' 1 have very low scores along RW4 being relatively similar to Mladeč 5 and Qafzeh 1.

The analysis of the supraorbital region for the complete sample generally confirms the earlier results received for the complete frontal bone. Neanderthals and recent modern humans appear to display different ontogenetic trends in the supraorbital region that start at dissimilar shapes in the youngest individuals in the analysis and then diverge in the space of the first two components. However, there is greater overlap between Neanderthals and other archaic and, in a few cases, Upper Palaeolithic forms than in the analysis of the complete frontal bone. The overlap is driven by such fossils as Předmostí 3, Qafzeh 6, Singa and Skhodnya that fall within the range of the Neanderthal distribution in the space of the first two relative warps and Zuttiyeh and Khvalynsk along the second relative warp. Skhul V is found to be very different in the morphology of its supraorbital region from all modern humans and Neanderthals by the combination of the first four relative warps.

Among North-East Eurasian fossils, Skhodnya and Khvalynsk show a closer association with the 'archaic' forms than was obvious from the relative warp analysis of the complete frontal bone. The similarity of these two fossils to Skhul V, which was detected for the complete frontal bone, is not confirmed for the supraorbital region. To the contrary, Teshik-Tash confirms its ambiguous position between Upper Palaeolithic modern humans and

Neanderthals, that can possibly be resolved if juvenile forms of other 'archaic' hominins are included into the analysis. Sungir' 2, Sungir' 3 and Starosel'e are firmly associated with the recent modern children.

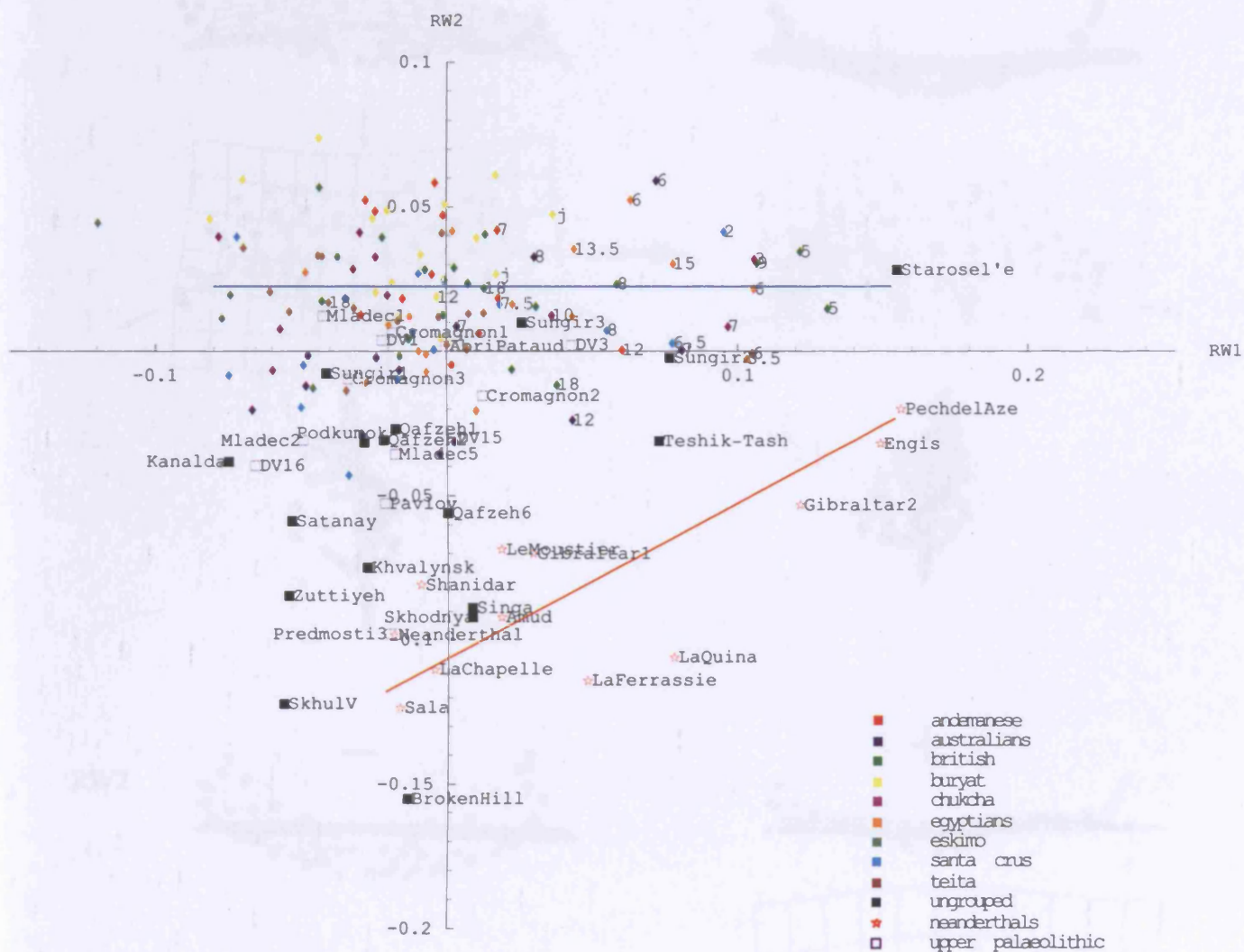


Figure 5.26a. 3D data for the supraorbital region. Ontogenetic dataset. Distribution of individuals in the space of the first and second relative warps. Recent sub-adults are additionally marked by their age. Blue and red lines highlight modern human and Neanderthal ontogenetic trajectories respectively.

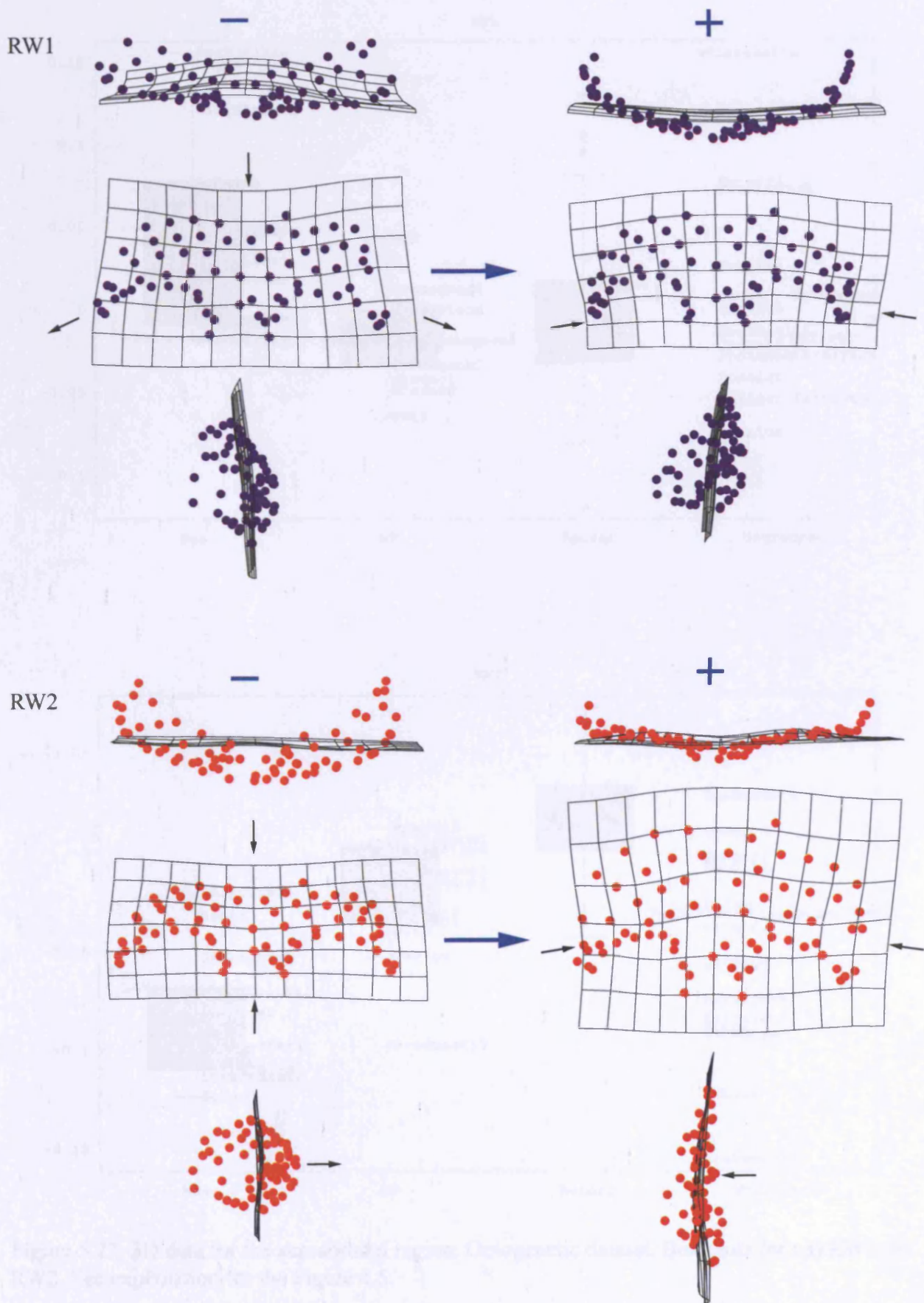


Figure 5.26b. 3D data for the supraorbital region. Ontogenetic dataset. First and second relative warps: morphological trends described. shape. TPS transformation of the consensus shape grid towards the target of a shape three standard deviations away from the consensus.

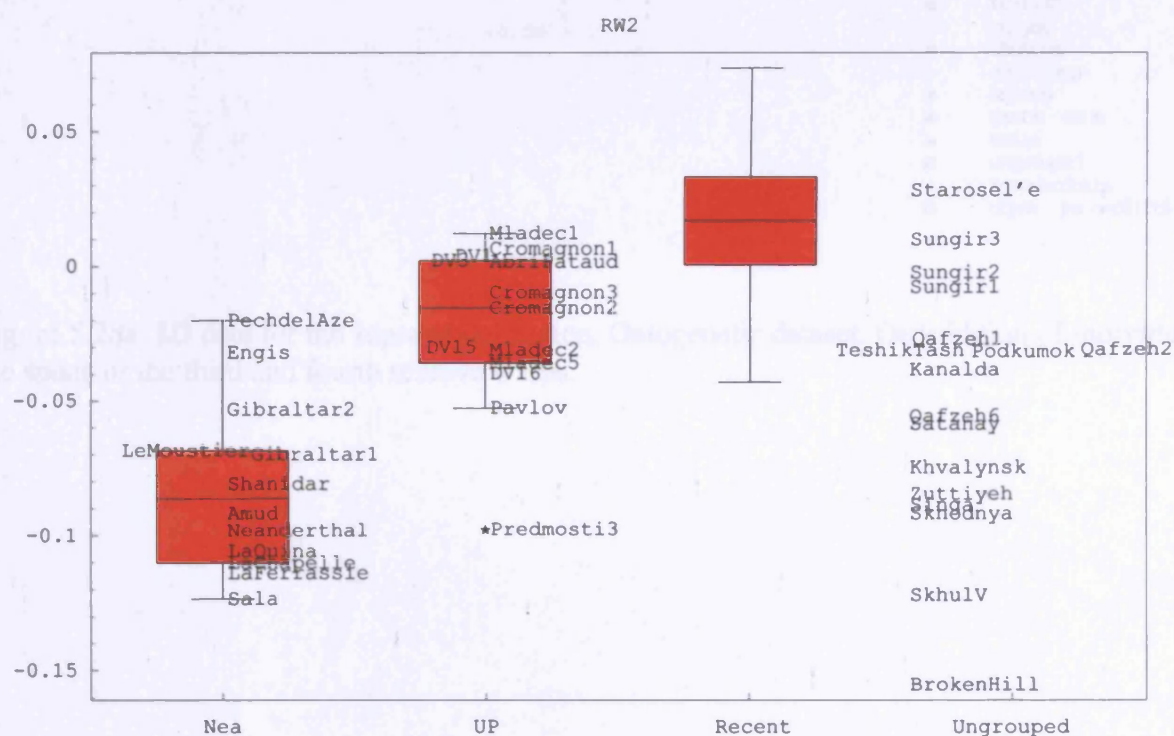
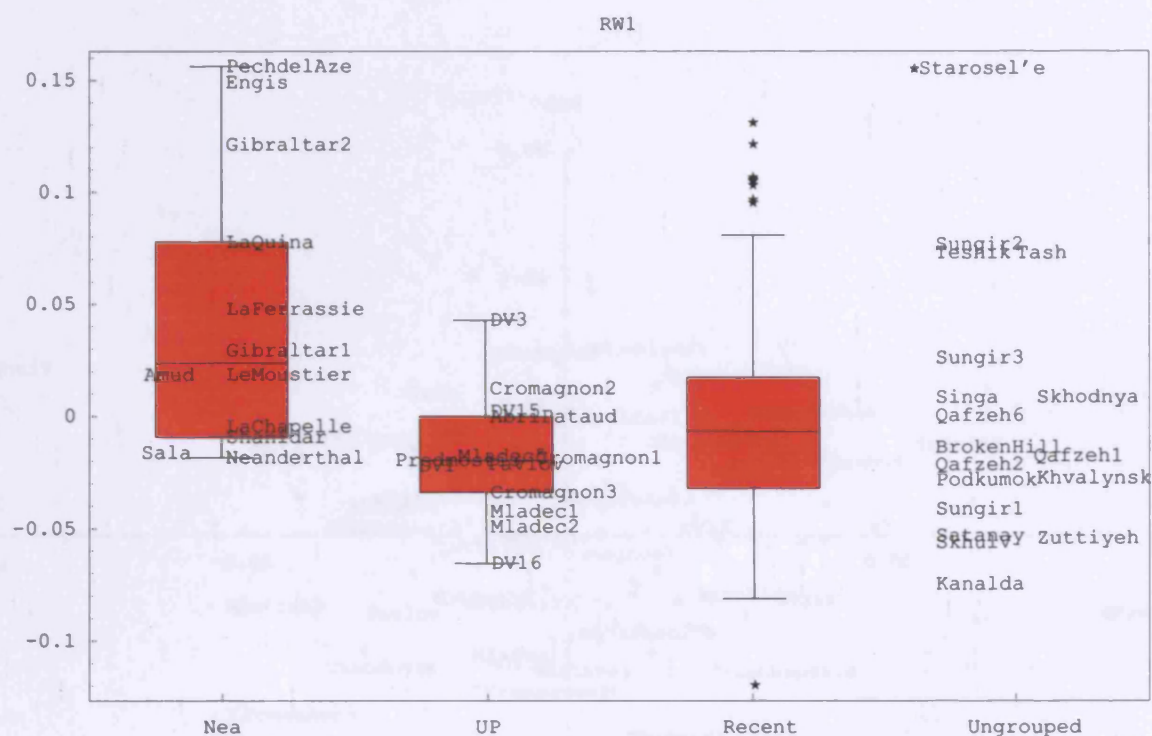


Figure 5.27. 3D data for the supraorbital region. Ontogenetic dataset. Box plots for : a) RW1; b) RW2. See explanation for the Figure 4.5.

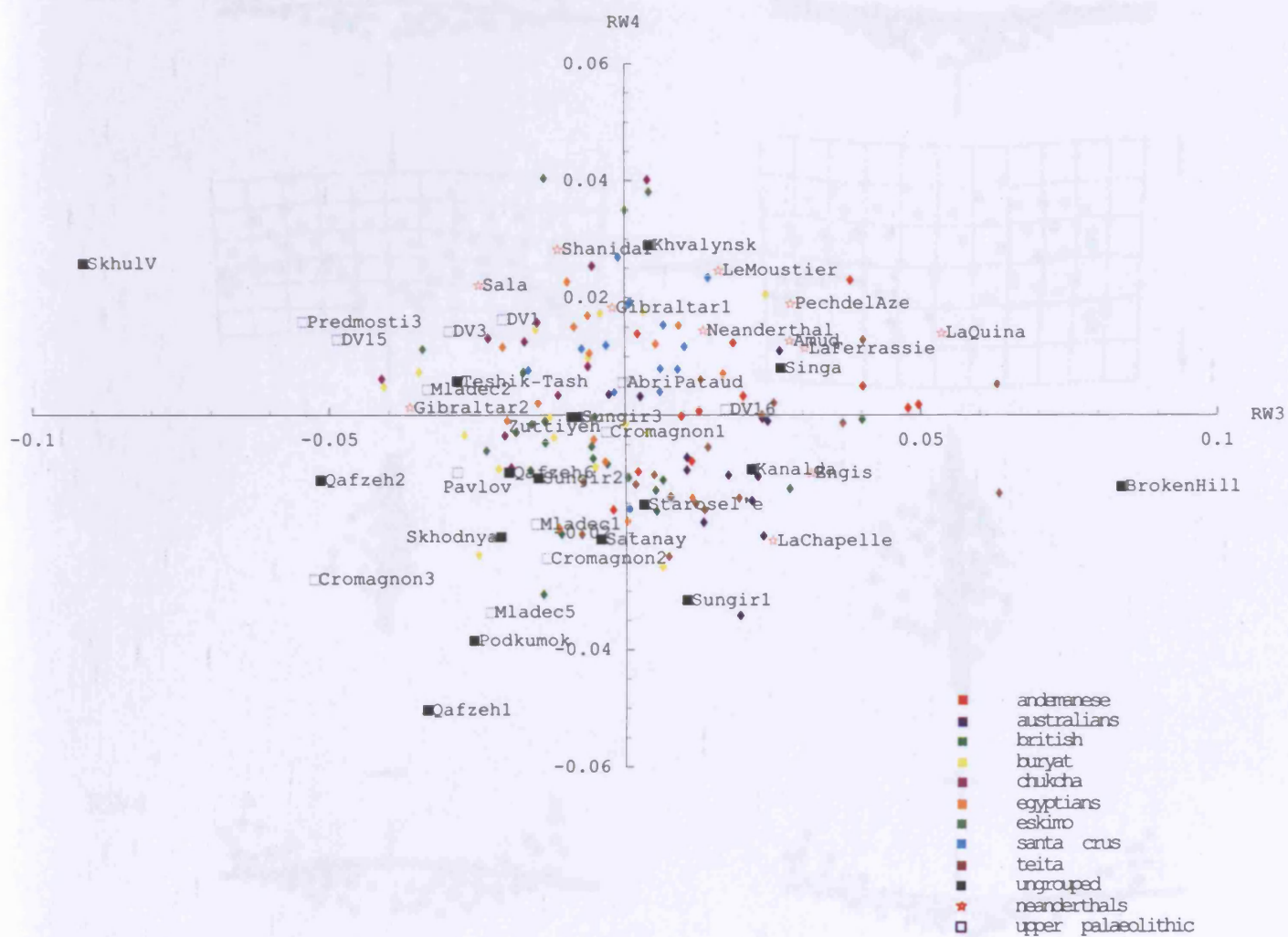


Figure 5.28a. 3D data for the supraorbital region. Ontogenetic dataset. Distribution of individuals in the space of the third and fourth relative warps.

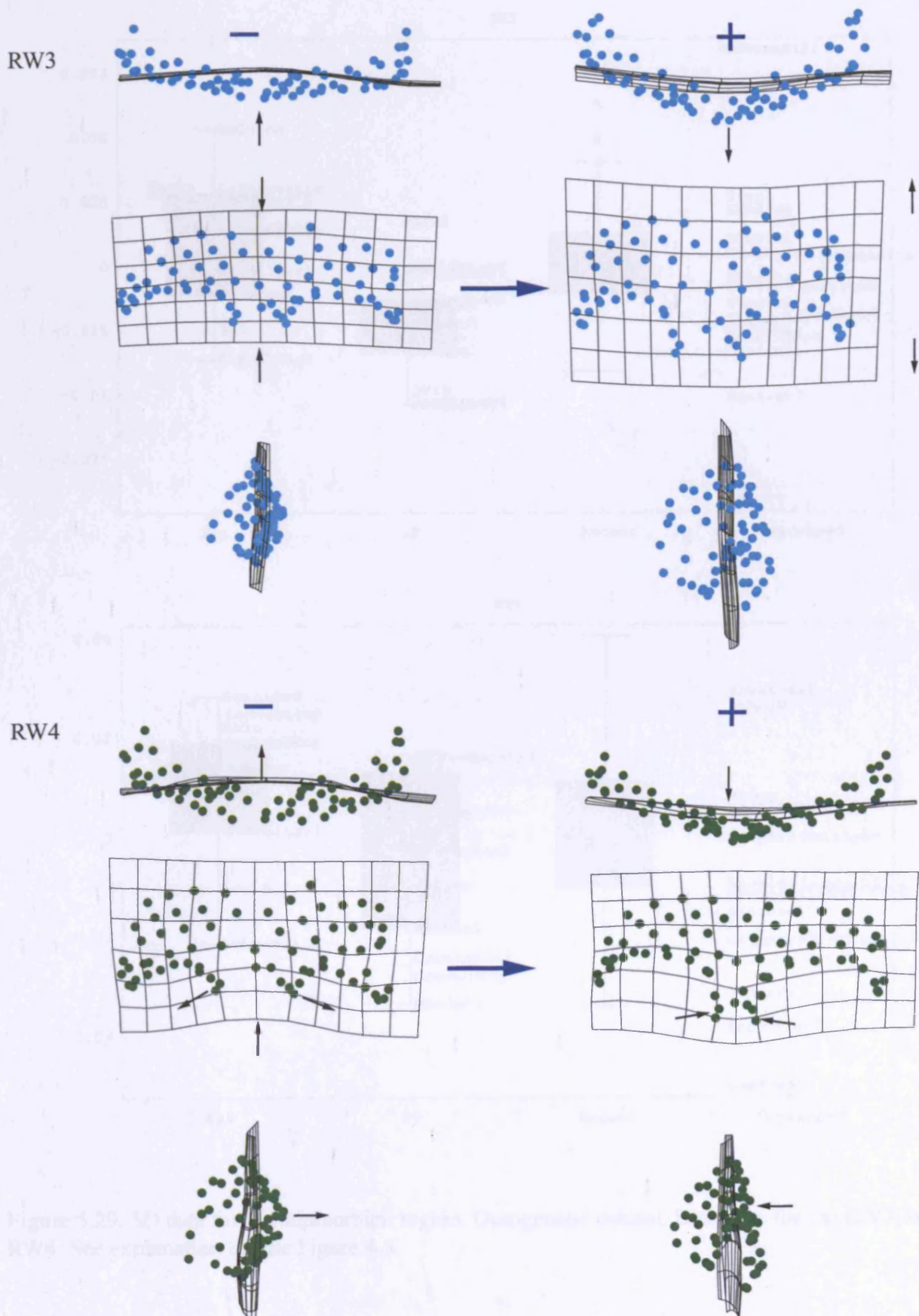


Figure 5.28b. 3D data for the supraorbital region. Ontogenetic dataset. Third and fourth relative warps: morphological trends described. shape. TPS transformation of the consensus shape grid towards the target of a shape three standard deviations away from the consensus.

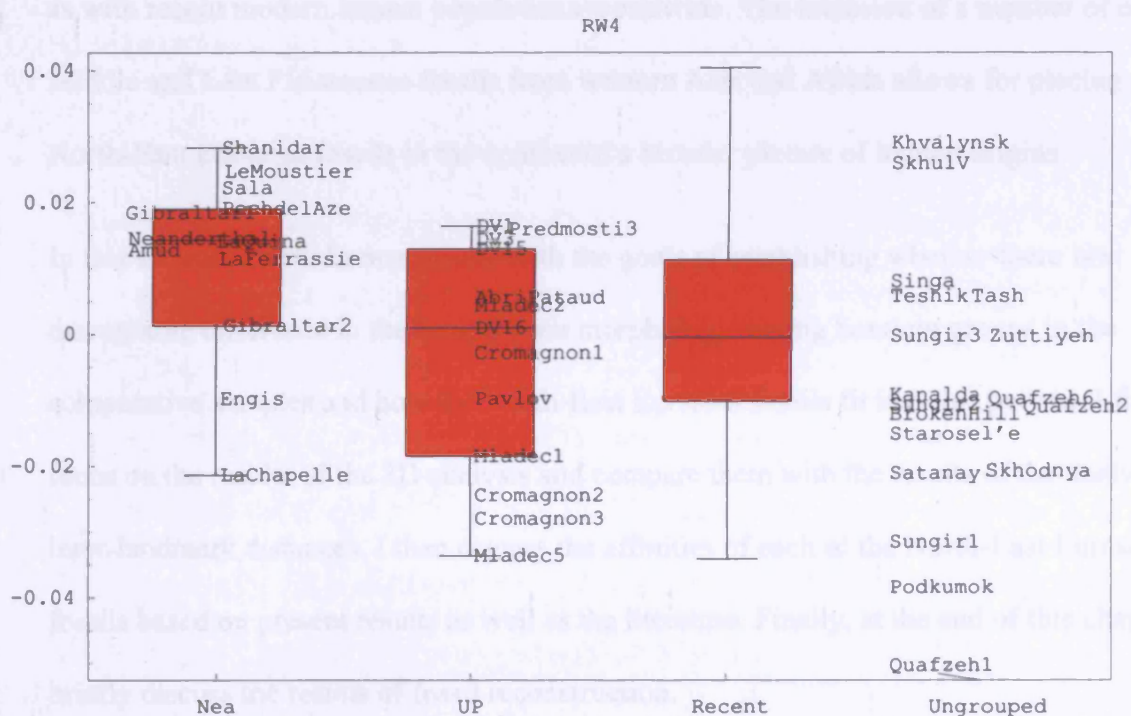
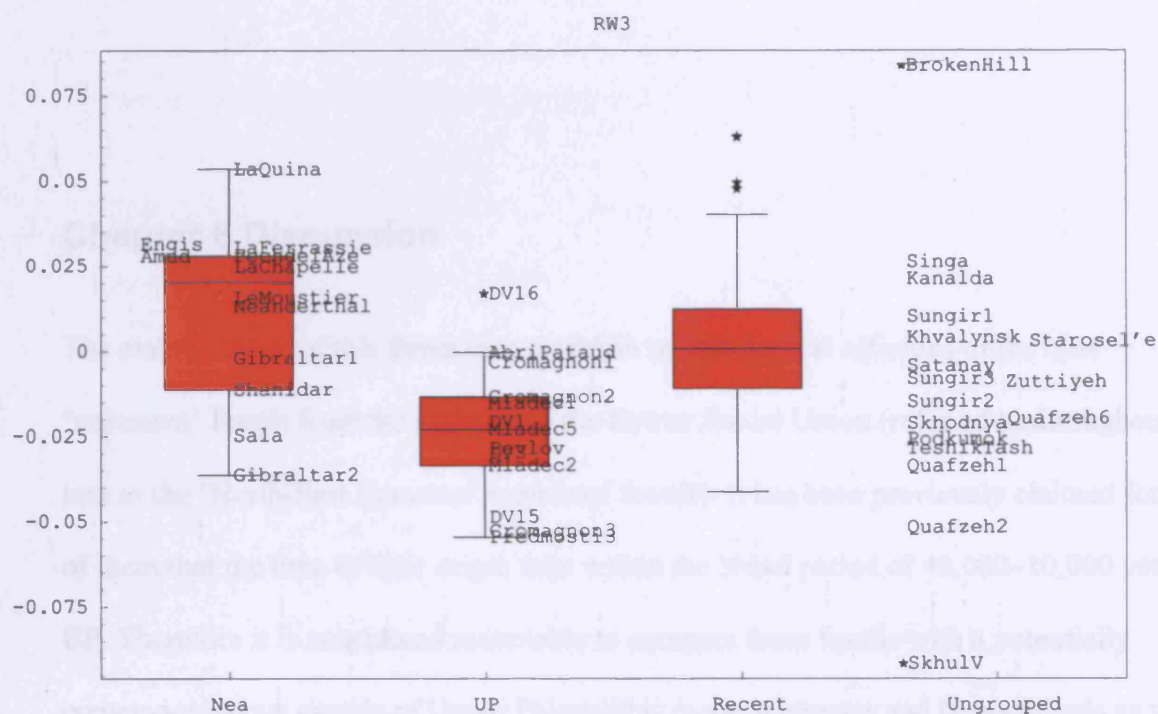


Figure 5.29. 3D data for the supraorbital region. Ontogenetic dataset. Box plots for : a) RW3; b) RW4. See explanation for the Figure 4.5.

Chapter 6 Discussion

The main purpose of this thesis is to establish morphological affinities of the nine ‘unknown’ fossils from the territory of the former Soviet Union (referred to throughout the text as the ‘North-East Eurasian’ sample of fossils). It has been previously claimed for each of them that the time of their origin falls within the broad period of 40,000–10,000 years BP. Therefore it is considered reasonable to compare these fossils with a potentially contemporaneous sample of Upper Palaeolithic modern humans and Neanderthals as well as with recent modern human populations worldwide. The inclusion of a number of other Middle and Late Pleistocene fossils from western Asia and Africa allows for placing the North-East Eurasian fossils in the context of a broader picture of human origins.

In this section, I will discuss results with the goals of establishing whether there is a discernable difference in the frontal bone morphology among hominin groups in the comparative samples and how the North-East Eurasian fossils fit into this pattern. I first focus on the results of the 3D analysis and compare them with the results of the analysis of inter-landmark distances. I then discuss the affinities of each of the North-East Eurasian fossils based on present results as well as the literature. Finally, at the end of this chapter I briefly discuss the results of fossil reconstruction.

Geometric morphometric analysis

The analysis of 3D data on the frontal bone generally differentiates between modern versus 'archaic' hominins. It also shows differences in the growth trajectories between Neanderthals and recent modern humans. However, given the observed overlap of the Neanderthals and other 'archaic' hominins in the sample a number of questions emerge about the validity of the Neanderthal autapomorphic morphologies in the frontal bone and their unique growth trajectory. All differences discussed in the 3D analysis are related to the shape of the frontal bone as opposed to the shape and size encoded in the inter-landmark distances.

Archaic vs. Modern forms

The best differentiation in the geometric morphometric analysis was found between the 'archaic' and 'modern' morphologies of the frontal bone. This is manifested by separation between anatomically modern human individuals (i.e. recent human populations and Upper Palaeolithic fossils) and a range of earlier Late Pleistocene fossils in both the relative warp and multidimensional scaling analyses. The main distinguishing features are mostly summarised in the second relative warp for the analysis of the complete frontal bone in adults and for the supraorbital region in all individuals. The first relative warp performs the same job in the analysis of the supraorbital relief in adults. The 'archaic' vector is manifested in a shorter, flat squama, which has a relatively smaller width than the expanded and protruding supraorbital relief in 'archaic' hominins. The supraorbital relief in the 'archaic' shapes is narrower in the cranio-caudal direction than in modern humans. There is also a tendency towards inflation of the supraorbital trigones and a smooth, rounded outline

of the supraorbital region that sweeps back laterally from the glabella. The ‘modern’ morphology as seen in each of the analyses includes slightly longer, curved squama of the frontal and a flat, tall supraorbital region that, in its ultimate expression, also has relatively flat superciliary arches. This morphology almost totally differentiates modern humans from all archaic hominins and is related to modern human autapomorphies of the neurocranial globularity and relatively flat supraorbital region (Stringer et al., 1984; Kidder et al., 1992; Lieberman et al., 2002; 2004; Stringer, 2002a; Trinkaus, 2006a). However, it is also the relative width of the frontal squama and the supraorbital region as well as the large height of the latter that differentiate modern human frontal bones from ‘archaic’ ones.

At the beginning of this study, I expected that Neanderthals would be distinct in frontal bone morphology from other groups in the sample. Hublin (1998, Table 1), for example, listed the following features that could be useful for establishing Neanderthal affinities of a frontal bone: rounded supraorbital torus without distinct elements, secondarily increased relative platycephaly (reflected in a low profile of the frontal squama), high orbits and low nasofrontal angle. Based on my quantitative analysis, however, the first two of these features are found in all Late Pleistocene hominins (albeit in differing degrees of expression). The height of the orbits was not evaluated in this analysis, but the low nasofrontal angle was important in distinguishing Neanderthals during the analysis of inter-landmark distances.

On the whole, the ‘archaic’ combination of features of the frontal bone surface is to different extents characteristic of the Neanderthals, the early anatomically modern humans from Levant (Qafzeh 6 and Skhul V) and Africa (Singa and Broken Hill) in opposition to the the majority of the Upper Palaeolithic and all recent modern humans. The present

analysis also demonstrated that the complete frontal bone separates Neanderthals more effectively than just the supraorbital region when compared to other Late Pleistocene hominins. In other words, Neanderthals and various other Late Pleistocene hominins overlap more strongly in the morphology of the supraorbital relief (Fig.5.17a) than in the shape of the complete frontal bone. This finding goes against expectation that the peculiarities of the Neanderthal browridges might provide for better discrimination of the group (Cunningham, 1908; Smith and Ranyard, 1980; Hublin, 1998). This difficulty to pinpoint Neanderthal autapomorphies in the browridge morphology, as described by Smith and Raynard (1980), may show that they are, in fact, generally primitive for Middle to Late Pleistocene hominin populations. Further investigation that includes fuller sample of late Pleistocene fossils is needed to confirm this hypothesis.

Broken Hill represents the maximum expression of the 'archaic' morphology in the sample, and the majority of European Neanderthals, such as La Ferrassie, Gibraltar 1, La Quina and La Chapelle aux Saints immediately follow it. The western Asian and eastern European Neanderthals (such as Amud, Shanidar and Šal'a) as well as Neanderthal (Feldhofer) fossils themselves are close to the modern human spread of variation, overlapping with other Late Pleistocene fossils from western Asia and Africa (Skhul V, Qafzeh 6, Singa and Zuttiyeh). This trend is better seen in the complete frontal bone morphology than in the shape of the browridges taken out of the context where overlap between all Late Pleistocene hominins is quite large so that such fossils as Předmostí 3, Skhodnya and Khvalynsk fall within the 'archaic' group.

The trend of broad overlap between the archaic populations confirms observations made by Smith and Raynard (1980) and Sládek *et al.* (2002). The former authors found a continuous

trend from more massive supraorbital relief in Neanderthals to less massive in European Upper Palaeolithic modern humans. Sládek *et al.* (2002) detected a similar trend among a wide range of Middle, Late Pleistocene and Holocene hominins using a scoring system for visual comparison of the morphology of the supraorbital region in Middle Palaeolithic fossils, Neanderthals, the Skhul/Qafzeh group and Early Upper Palaeolithic humans compared to the Šal'a frontal bone. According to Sládek *et al.* (2002), a trend exists towards reduction in the general size of the torus and its anterior projection, less frequent appearance of the sinusoid shape of the torus outline in *norma frontalis*, and thinning of the supraorbital margin across time from the Middle Upper Palaeolithic fossils to the Early Upper Palaeolithic. Neanderthals and the Skhul/Qafzeh sample have intermediate frequencies of the features. According to Sládek *et al.* (2002), only two characteristics seem to distinguish the Neanderthal sample: a rounded connection between torus and orbit and the absence of a sulcus in the supraorbital area. Neanderthals also have a somehow elevated frequency of the rounded shape of the orbits (Table 2, Sládek *et al.*, 2002). In the present study, however, these features did not have any strong influence on the first several relative warps in the present study.

The 'archaic' group of hominins also demonstrates a cline that is partly in agreement with earlier observations on the lesser expression of the Neanderthal autapomorphies in the western Asian and eastern European Neanderthals (Jelínek, 1969; 1982b; Smith, 1984; Wolpoff and Caspari, 1990; Trinkaus, 1991; Corruccini, 1992; Kidder *et al.*, 1992). This cline is better observed in the morphology of the complete frontal bone surface than in the supraorbital relief alone. The latter results questioned the discriminative power of the supraorbital morphology does not have as much discriminative power in the archaic fossils.

Upper Palaeolithic modern humans

For the purposes of the present work, it was important to establish whether recent modern humans differ significantly from the European sample of the Upper Palaeolithic modern humans. A number of previous studies have investigated this question explicitly or implicitly in the context of the debate on the modern human origins. For example Howells (1989), van Vark *et al.* (1992) and Lahr (1996) found differences between recent modern humans and Upper Palaeolithic populations in the morphology of the complete cranium. Van Vark *et al.* (1992) also demonstrated a cline of variation in Late Pleistocene and Holocene modern humans, with late Upper Palaeolithic humans being intermediate between earlier Upper Palaeolithic populations and later Mesolithic humans. Regarding frontal bone morphology in particular, Sládek *et al.* (2002) have shown significant differentiation between their Upper Palaeolithic sample and their recent populations in a multivariate analysis of inter-landmark measurements.

In the present study, permutation and discriminant analyses of group differences show significant differences between the modern Upper Palaeolithic individuals and a pooled sample of the nine recent modern human populations. These differences are based on features expressed by a number of relative warps as revealed by discriminant analysis. Some of these morphological differences are related to the transversely narrower, curved frontal bones as well as to the vertically short supraorbital region with more developed relief that is especially pronounced in the Moravian sample (Dolní Věstonice and Pavlov individuals). Variation among Upper Palaeolithic individuals is enhanced by the large expression of supraorbital relief in Předmostí 3, which caused it to be misclassified as Neanderthal in the analysis of the supraorbital region.

Differences between the two groups of modern humans raise interesting questions for discussion. First of all, is there any temporal or geographical pattern in the variation within the Upper Palaeolithic group? Secondly, do they represent real differences between Upper Palaeolithic and recent modern humans, or are they an artefact due to the limited Upper Palaeolithic sample in the analysis (e.g. mostly Moravian and Dordogne Upper Palaeolithic fossils are represented here)?

As it was shown by multidimensional scaling and discriminant analyses, the Dolní Věstonice and Pavlov sample of individuals and in some cases Cro-Magnon 1 and 2, Mladeč 2 and Předmostí 3 have some pronounced differences from recent humans. With the exception of the supraorbital relief in Předmostí 3, differences of the listed Upper Palaeolithic individuals from recent humans have common vectors. As a result, these vectors are picked up by Discriminant analysis, which demonstrated that DV1, DV3, DV15, DV16, Pavlov, Mladeč 2, and Cro-Magnon 1 and 2 for the complete frontal; DV3, DV15, DV16, Pavlov, Cro-Magnon 1, 2 and 3 and Mladeč 5 for the supraorbital relief, discriminate from recent modern humans as well as from Neanderthals. Therefore, these analyses suggest that there is a consistent difference between Upper Palaeolithic individuals and recent modern humans in the shape of the frontal bone, even in the face of the large spread of variation in the latter. These differences are not related to the elevated robusticity of the European fossils in the late Pleistocene as suggested by Lahr (1996) given that such relatively gracile individuals as DV1, DV3 and Mladeč 2 show the same differences from recent populations as do their more robust counterparts. Moreover, given that the Upper Palaeolithic sample here comes from two populations that are geographically separated by the Alps, these common trends in frontal bone morphology suggests that real differences exist between

recent and Upper Palaeolithic populations. Unfortunately, sampling of Upper Palaeolithic modern humans from only two areas in eastern and western Europe limits the power of interpretation. However, if Podkumok, the poorly dated fossil from the North Caucasus, is confirmed to have an Upper Palaeolithic date, its strong association with the morphology of the Moravian and Cro-Magnon Upper Palaeolithic samples would argue for the broad geographical dispersal of the distinctive Upper Palaeolithic modern human frontal bone features.

There is a pattern in variation of the Upper Palaeolithic sample from the chronological standpoint. The oldest Upper Palaeolithic sample from Mladeč, Moravia (about 31,000 years of age, see Wild *et al.*, 2005). Mladeč individuals show less pronounced differences from recent humans than the later individuals from the same region at Dolní Věstonice and Pavlov. The Dolní Věstonice group of fossils is directly dated to a later date of about 26,000–25,000 radiocarbon years BP (Svoboda *et al.*, 1996). Pavlov may date to 26,000 radiocarbon years BP by its stratigraphic context (Klima and Kukla, 1963; cited by Schwartz and Tattersall, 2002). Therefore, the differentiation of the later Moravian sample may result from isolation and genetic drift in the region.

At the same time, the French fossils from Cro-Magnon also demonstrate differences from recent modern humans but to a lesser extent than the late Moravian fossils. They are similar to Dolní Věstonice in the shape of the complete frontal bone but not in the details of the shape of the supraorbital relief. Cro-Magnon individuals are currently directly dated to about 27,000 radiocarbon years BP (Henry-Gambier, 2002) and therefore are broadly contemporaneous with the later Moravian sample.

As it is shown above, the earliest modern humans in Europe (Mladeč) could have had more generalised morphology of the frontal bone than the immediate descendants of the first modern human colonists in Europe. However, later Upper Palaeolithic humans, such as Abri Pataud and Sungir' in the present comparative sample are different from the previous generations of modern humans in Europe and are virtually indistinguishable from recent modern humans. Abri Pataud is at the moment dated by the AMS date of the stratigraphic level where it was found to about 22,000 radiocarbon years BP (Briker and Mellars, 1987, cited by Schwartz and Tattersall, 2002). This corresponds well with the date of Sungir' individuals that may lie between 19,160 (for Sungir' 1) and 27,210 (for Sungir' 3) radiocarbon years by direct dating (Kuzmin et al., 2004).

One fossil is inconsistent with the time cline: Předmostí 3, whose supraorbital relief aligns it with archaic hominins. Předmostí may date to about 26,000 years BP as was found on the basis of the revisited stratigraphy of the site (Allsworth-Jones, 1986; Vlcek, 1991; Jelínek, 1991, cited by Schwartz and Tattersall, 2002). It is difficult to judge the origin of the archaic features of the Předmostí 3 supraorbital relief. Proponents of the dispersal with admixture hypothesis consider these features to be obtained by gene flow from Neanderthals in this region (see, for example Trinkaus et al., 2003). In my opinion, this suggestion is impossible to verify on the basis of the morphological analysis presented in this thesis. First, information about the fine detail of the supraorbital relief, such as the discernable division between superciliary arches and supraorbital trigone, may have been lost during the general quantification of the surface, especially given the development of lateral portions of supraorbital relief in Předmostí 3. Secondly, Předmostí 3 also behaves as an outlier to its *a-priori* Upper Palaeolithic group in the discriminant analysis of the

complete frontal bone. To summarise, the disclosed differences are probably representative of a real morphological distinction between Upper Palaeolithic modern humans in Europe and recent modern human populations around the world. There is also differentiation within the Upper Palaeolithic sample in the present analysis that that may correspond to traces of the initial migration of the early modern humans into Europe (Mladeč forms), genetic drift in local areas (Dolní Věstonice and Pavlov as opposed to Cro-Magnon) and subsequent homogenisation of the European Upper Palaeolithic population. Processes supporting homogenisation would be gene flow and migration at different stages of the climate and landscape development during and after the last glacial maximum.

Recent modern human populations

The composition of the comparative sample of the recent populations was intended to represent worldwide variation in frontal bone morphology in recent modern humans. A generally high overlap in frontal bone morphology was detected among populations throughout the course of the analyses. All recent modern humans share frontal bone morphology together with the Upper Palaeolithic individuals, in opposition to Neanderthals and other Late Pleistocene hominins in the comparative sample. However, as was argued above, Upper Palaeolithic fossils from Europe can be distinguished from recent modern humans even in the face of relatively large variation in the latter.

West Asian Late Pleistocene hominins

West Asian Middle and Late Pleistocene hominins have been crucially important in the argument over modern human origins (see, for example, a review in Stringer, 2002). Due to their geographical location, the Levant and Zagros mountains connect the ancestral

continent of Africa with Europe and the rest of Asia, creating an essential bridge that would have been impossible to bypass during hominin expansion. In order to contextualise the results presented here, I offer a brief review of the dating and morphology of the frontal in the west Asian sample of hominins.

According to Bar-Yosef (2000), Middle Palaeolithic technologies prevailed in this region from 270,000 to 250,000 years BP until perhaps slightly later than 50,000 years BP and were followed by a swift 'Upper Palaeolithic revolution' at about 47,000–46,000 radiocarbon years BP. The latter could either develop *in situ* from the local Middle Palaeolithic or be brought from other lands, such as East Africa and the Nile Valley (Bar-Yosef, 2000). In any case, the most dramatic events of migration, co-existence and evolution of different hominins in west Asia were happening within the framework of the Middle Palaeolithic.

The only exception from the Middle Palaeolithic fossil record in the Levant is the Zuttiyeh hominin that was discovered in the course of excavations at Mugharet el-Zuttiyeh in 1925 in association with Acheulo-Yabrudian industry (Keith, 1927; Turville-Petre, 1927).

Zuttiyeh is the oldest known hominin fossil from the Levant and is dated to about 200,000–280,000 years BP (Vandermeersch, 1981b; 1989; Bar-Yosef and Vandermeersch, 1993; Bar-Yosef, 1995). Hominin remains from Zuttiyeh primarily consist of frontal bone and a part of a zygomatic bone belonging to one individual. The taxonomical status of Zuttiyeh has been contentious from the moment of its discovery, when it was assigned to Neanderthals (Keith, 1927). Simmons *et al.* (1991) considered Zuttiyeh as an ancestor of West Asian Neanderthals on the basis of the frontal bone measurements. Hublin (1998) found that this fossil does not display Neanderthal affinities at a time when Neanderthal

derived features are already observed among European hominins. Sohn and Woploff (1993) found that the differences that distinguish Zuttiyeh from Neandertals are similarities it shares with the Zhoukoudian remains interpreting them as suggestive of ancestral relationship between the eastern and western Asian hominins. Finally, Zeitoun (2001) concluded that Zuttiyeh can be attributed to modern humans on the basis of a cladistic analysis features of the frontal and the zygomatic fragment.

The next oldest group of west Asian fossil hominins is possibly represented by fossils from Skhul, Qafzeh and Tabun, which are now dated to about 100,000–130,000 years BP (Grün et al., 2005). The Tabun site yielded a number of mainly fragmentary remains of Neanderthals (Garrod and Bate, 1937; McCown and Keith, 1939; Neuville, 1951), two of which, Tabun C1 (an almost complete cranium and partial postcranial remains of a female) and Tabun II (a mandible), are the best preserved specimens. Skhul and Qafzeh sites provided a large number of hominin remains, totalling 13 adults and 11 children. The majority of these fossils are associated with Middle Palaeolithic industry, but Qafzeh 1 and 2 may belong to an Upper Palaeolithic level from the cave (Bar-Yosef, 2000).

The modern human characteristics of the Skhul and Qafzeh fossils were identified at the time of their discovery (McCown and Keith, 1939). Subsequent studies concentrated on interpreting the combination of modern and 'archaic' features in these fossils, which are expressed to a different extent among the specimens (see, for example, Vandermeersch, 1981a; 1981b; 1989; 1969; Tiller, 1989; 1999; Wolpoff, 1999; Corruccini, 1990; 1992; Trinkaus, 1984; Stringer, 1992a; Turbon et al., 1997). Currently, the prevailing opinion has shifted towards interpreting these fossils as representatives of the early Anatomically Modern humans who first appeared in Africa at the time around 200,000–150,000 years BP

and then spread around the world between 60,000 and 40,000 years BP (Stringer and Andrews, 1988; Hublin, 1998;Stringer, 2000). In this scenario, Skhul and Qafzeh hominins actually belong to initial African pool of early modern humans (Lahr, 1996; Trinkaus, 2005).

The west Asian fossils from the time between 80,000 and 50,000 years BP all belong to the Neanderthal group and consist of Middle Palaeolithic fossils from Shanidar (Zagros Mountains, Iraq), Dederiyeh (Syria), Kebara and Amud sites (Israel) (Suzuki and Takai, 1970; Trinkaus, 1983; Bar-Yosef et al., 1992; Akazawa et al., 1993; Bar-Yosef, 2000). One important characteristic of the west Asian Neanderthals is a lesser degree of expression of some Neanderthal autapomorphic features compared to their West European counterparts (see, for example, Trinkaus, 1983; 1984). In the course of the 1980s, this observation allowed a number of authors to construct a temporal and morphological sequence from an earlier archaic human stage, through a later archaic human stage (“typical” Neanderthal), to early modern humans (Wolpoff, 1980; Jelínek, 1982a; 1982b; Trinkaus, 1983; 1984; Smith, 1985). This model was overturned by before thermoluminescence (TL) and electron spin resonance (ESR) dating of Qafzeh and Skhul hominins, which confirmed that these presumed anatomically modern humans were older than the majority of the west Asian Neanderthals (Schwarcz et al., 1988; 1998; Stringer et al., 1989; Valladas et al., 1987;1988)

There is a certain amount of disagreement between different authors on how distinctive the early Anatomically Modern humans are from western Asian Neanderthals. Corruccini (1990; 1992), for example, argues that the ‘forgotten skulls’ Skhul IX and Skhul IV are in fact very similar to the west Asian Neanderthals in morphology and show ‘modern’ apomorphies to a lesser extent than Skhul V and Qafzeh 6. He suggests that all Middle

Palaeolithic hominins from west Asia belong to a single, albeit very diverse, group. On the other hand, Stringer (1992b) shows a distinctive dichotomy in skull morphologies between west Asian Neanderthals and early Anatomically Modern Humans (the latter group included Skhul V and IX as well as Qafzeh 3, 6 and 9), with the Skhul/Qafzeh sample providing for a good shape intermediate between the archaic and recent sample. A similar dichotomy was detected by Holliday (2000) for the postcranial skeleton.

Contrary to these studies, I did not find a clear dichotomy of frontal bone morphology within the west Asian sample of hominins where there is relatively wide variation from Neanderthal-like to human-like. Skhul V is found especially different due to the ‘pinched’ sagittal profile of its browridge, relatively long coronal suture and posterior position of bregma. However, considering the modern-archaic vector of the shape differences in the sample, all west Asian hominins cluster closely together between fossils with more prominent browridges and flatter frontals (La Ferrassie, La Chapelle aux Saints, Gibraltar 1, Broken Hill) and modern humans in Multidimensional Scaling (Fig.5.14a) or overlap with Neanderthal and Šal’a in the relative warp analysis (Fig.5.10a). Amud 1 and Shanidar 1 have a very similar shape of frontal, consistent with the fact that they have both been considered Neanderthals. Together with Skhul V, which differs from them in subtle aspects of morphology, Amud 1 and Shanidar 1 are similar to such European Neanderthals as La Chapelle aux Saints, La Ferrassie, La Quina and Gibraltar 1. Singa is very close the west Asian fossils in the morphology of the frontal. Qafzeh 6 and Zuttiyeh express less ‘archaic’ morphology but so do Šal’a and Neanderthal. Unlike other west Asian hominins in the analysis, Qafzeh 1 and 2 are firmly associated with modern humans. The results of discrimination have shown that Qafzeh 1 may be more similar to the Upper Palaeolithic

fossils in the shape of the complete frontal, whereas Qafzeh 2 is more similar to them in the shape of the supraorbital relief. These results agree with the possibility of their Upper Palaeolithic origin (Bar-Yosef, 2000).

The result of the analysis of the supraorbital region suggests a similar pattern. In the analysis of the supraorbital region, Qafzeh 6 was found to possess less robust supraorbital relief even in comparison with Skhul V, and it is more similar to modern humans (see, for example, the results of the Multidimensional Scaling, Fig. 5.21a).

In some respects, these results agree with the paper by Simmons *et al.* (1991). One of the most striking features of this analysis is the overlap of some Neanderthals and early modern humans in principal component analysis. Thus, according to Figure 3 in Simmons *et al.* (1991), Skhul 9, Qafzeh 6, Skhul IV, Zuttiyeh, Shanidar 1, Amud and Skhul V form a relatively tight cluster with Tabun C1 being the closest to them. This group is distinct from Qafzeh 1, 2 and 9 on one hand and Shanidar 5 on the other. Although Simmons *et al.* (1991) come to the 'modern' interpretation of the Skhul/Qafzeh sample as opposed to seeing 'Neanderthal' affinities, as well as the closer association of Zuttiyeh with west Asian Neanderthals, their conclusion is not directly supported by their principal component analysis of the frontal bone shape.

The range of variation within west Asian hominins is therefore not easily resolvable within the framework of the three chosen *a priori* groups: recent modern humans, Upper Palaeolithic modern humans and Neanderthals. This is particularly seen in results of the discriminant analysis. By the design of the analysis, Shanidar 1 and Amud 1 were included into the *a priori* Neanderthal group. It was expected that the early Anatomically Modern

humans Skhul V and Qafzeh 6 would better associate with the recent and Upper Palaeolithic modern humans, whereas Zuttiyeh would be found intermediate as an ancestral, less derived form. However, all these fossils, including Qafzeh 6, Skhul V and Zuttiyeh, are ultimately intermediate between Neanderthals and modern human groups. Their classification into one of the three *a-priori* groups is not certain in most cases. Classification of Skhul V is the least successful, as it behaved as an outlier in all analyses. Qafzeh 6 is classified as a Neanderthal in both discriminant analyses, for the complete frontal and for the supraorbital region. Even though the distances between Qafzeh 6 and the centre of Neanderthal populations are higher than the maximum distance within Neanderthals, they are comparable with the distances within the two other *a-priori* groups. Zuttiyeh shows differing classifications: recent modern human based on the complete frontal, and Neanderthal based on only the supraorbital region.

In sum, the present results argue against a clear modern-Neanderthal dichotomy in the morphology of the frontal bone in the west Asian hominins. However, the variation in frontal bone morphology by itself cannot test the presence of such a dichotomy in other parts of the skeleton (Stringer, 1992b; Holliday, 2000). Interestingly, the African Late Pleistocene fossil from Singa overlaps with west Asian hominins in frontal bone morphology suggesting either their common ancestry or genetic connections between African and west Asian groups. The overall pattern indicates the African connection of the west Asian hominins.

Ontogenetic patterns

Many authors have postulated that specific Neanderthal features appear early in the Neanderthal ontogeny (e.g., Tiller, 1989). With regard to the frontal bone, Smith and Ranyard (1980) describe continuous extension of the supraorbital torus across the orbits and interorbital area in specimens that are younger than 6 or 7 years of age, although this morphology is only visible as a slight bulging from the squama. Younger specimens seem to have some division between toral segments. Older subadults, like Le Moustier (estimated 15 years old) and Krapina cranium E exhibit tori very close in overall form and size to those of adults, but they lack the final aspects of the growth and remodelling process that produces the characteristic Neanderthal torus. Le Moustier has been suggested as a type adolescent individual for determination of Neanderthal features on fragmentary material (Ahern and Smith, 2004).

Ponce de Leon and Zollikofer (2001) present results of a multivariate analysis of 3D anatomical landmarks on the skull (51) and mandible (22) in a sample of recent modern human populations all over the world, anatomically modern humans from western Asia (Skhul 1, Qafzeh 11 and Qafzeh 9) and Neanderthals (16 individuals). They find significant differences between growth trajectories in recent modern humans and Neanderthals. These differences are already present by the dental stage two (after eruption of the lower deciduous canine but before full crown development of I1) and remain subsequently unchanged during ontogeny. Thus, according to Ponce de Leon and Zollikofer (2001), the modern human and Neanderthal ontogenetic trajectories are parallel.

Among features relevant to the shape of the frontal bone is the shape of the cranial vault: low, posteriorly expanded cranial vault in Neanderthals and increased drift and displacement in its inferior region, which, according to these authors, may account for many of the Neanderthal apomorphies (broadened temporal regions, rounded lateral cranial vaults, a more caudal position of the middle cranial fossa, an elongated foramen magnum, and a large occipital squama). In Figure 4 of Ponce de Leon and Zollikofer (2001), one can observe that, at the tooth development stage two, the major features of the Neanderthal frontal bone include a lower frontal squama, more growth in the temporal areas and in the areas of the supraorbital arches. Modern humans, on the other hand, have higher and steeper foreheads and relatively less growth in the growth fields of the supraorbital region.

Distinctive growth trends are also found for recent modern humans and Neanderthals in the results presented here. As in Ponce de Leon and Zollikofer (2001), Neanderthals as young as 2.5 years of age (Pech de l'Aze) are already different from recent modern humans in both complete frontal bone morphology and the shape of the supraorbital region. However, in contrast with the findings by Ponce de Leon and Zollikofer (2001), the frontal bone growth trajectories are not parallel in recent modern humans and Neanderthals. As shown by relative warp analyses, Neanderthal growth markedly diverges from the recent modern human trend resulting in relatively larger differences in adults than in children of the two species.

The composition of the dataset here is slightly different from that used by Ponce de Leon and Zollikofer (2001). It includes a number of Late Pleistocene fossils from west Asia and Africa that are absent from their analysis (Skhul V, Qafzeh 6, Singa, Broken Hill) but lacks others that were present in the earlier study (early modern humans Qafzeh 11 and Qafzeh 9,

with Skhul 1 is represented only by a mandible, as well as Amud 7, Poc de Marsal and La Naulette Neanderthals). Therefore, some of the differences in the results may be accounted for by the different datasets. Nevertheless, it has been expected that the general growth trends of same-species hominins would stay the same regardless of the sample differences.

However, the present analysis demonstrated that the general ‘archaic’ features that distinguish Neanderthal frontal bones from modern humans are not unique for the Neanderthals. In the ontogenetic analysis of the complete frontal bone, fossils such as Qafzeh 6, Skhul V, Singa and Zuttiyeh overlap with Šal’a, Shanidar and Le Moustier along this shape component. The frontal bone of the Broken Hill fossil has even more pronounced expression of the ‘archaic’ features than in Neanderthals. The outcome of the analysis of the supraorbital relief is more ambiguous. Broken Hill, Skhul V, Předmostí 3, Khvalynsk, Skhodnya, Singa and Zuttiyeh, all overlap with the Neanderthal distribution along the relative warp describing the ‘archaic’ trend in morphology. It is quite possible, that the ontogenetic trends of different groups of archaic hominins would also overlap, provided a sufficiently large sample of Late Pleistocene fossils of different ages is assembled. As a result, the Neanderthal ontogenetic trajectory, as identified by Ponce de Leon and Zollikofer (2001), would be very similar if not the same for all Late Pleistocene ‘archaic’ hominines.

Summary of the 3D analysis

A consistent pattern of variation within the comparative sample has been revealed in the course of the analysis of the 3D surface data for the frontal bone in Late Pleistocene and Holocene hominins. First of all, marked differences are detected between modern and

‘archaic’ shape of the frontal. The first type is characteristic of the recent and the majority of the Upper Palaeolithic modern humans, whereas the second is an attribute of Neanderthals, west Asian early modern humans and African representatives, such as Broken Hill and Singa. In this context, it is not easy to pinpoint apomorphies that would distinguish all Neanderthals as a group from other ‘archaic’ hominins in the sample, contrary to previous suggestions, such as by Ahern and Smith (2004) or Sládek *et al.* (2000). The former authors employ the feature of a more rounded outline of the supraorbital margin in Neanderthals to distinguish them from such African fossils as KRM 16425 from Klasies River Mouth. The latter paper cites a rounded connection between torus and orbit and the absence of a supraorbital sulcus as features most frequently found in Neanderthals.

Nevertheless, the three groups defined throughout the present study -- Neanderthals, Upper Palaeolithic modern humans -- and recent modern humans show significant differences as demonstrated by the permutation tests and discriminant analyses, and thus they allow for classification of a number of ‘unknown’ individuals, including the North-East Eurasian fossils. However, the morphological affinities of the west Asian fossils have been found difficult to resolve within this analysis design pointing to the possibility of similar difficulties in classification of the unknown and, in the majority, badly dated fossils from the north-eastern Eurasia.

It has been found that Neanderthals and recent modern humans have different trajectories of frontal bone development. The differences between the two species are already noticeable by the age of two and further enhanced by the divergence of the frontal bone growth trajectories resulting in larger differences between adults than between children of

the two species. This picture facilitates attempts to find species affiliations of the immature fossil individuals in the North-East Eurasian sample. However, the overlap found in the relative warp analysis between Neanderthals and other adult 'archaic' hominins in the sample points to the possible difficulties of the unambiguous differentiation of Neanderthal and other 'archaic' children, such as immature individuals from African and west Asian collection of Late Pleistocene hominins, if those are ever included in the analysis as well as a possibility of an overlap in the ontogenetic trajectories between Neanderthals and other 'archaic' Late Pleistocene hominins.

Inter-landmark distances

The analysis of inter-landmark distances allowed an assessment of the dataset by multivariate analysis of traditional morphometric measurements and a comparison to geometric morphometric analysis using more traditional techniques. The limited reconstruction that has been done for the bilateral landmarks helped to increase the number of analysed measurements without compromising the sample size.

The results are also similar to the 3D geometric morphometric methods on differentiation between modern and archaic hominins. It is also in agreement with previous analysis of frontal bone morphology that used multivariate statistics of inter-landmark measurements (Sládek *et al.*, 2002). The previous study used a wider dataset of fossils, including Middle and Late Pleistocene fossils from Europe and west Asian and a larger sample of Upper Palaeolithic individuals than here. However, (Sládek *et al.*, 2002) employed only four measurements in their analysis that account for the general proportions of the frontal bone

(Minimum frontal breadth, Maximum frontal breadth, Frontal sagittal arc and Frontal sagittal chord).

The portrayal of hominin distribution by Sládek *et al.* (2002) shows significant separation between modern and archaic hominins. Skhul/Qafzeh fall within the archaic group (Middle Pleistocene fossils and Neanderthals in that study) but also showed some similarity to the Upper Palaeolithic sample. The discriminant analysis in Sládek *et al.* (2002) found that the most separation between groups is achieved by differences in minimum and maximum frontal breadths and the frontal sagittal arc. However, the archaic groups (i.e. Neanderthals and Middle Palaeolithic fossils) do not separate well in their analysis.

In the present study, the differentiation between the ‘archaic’ hominins and recent modern humans is supported by frontal angles from nasion and glabella, frontal sagittal arcs from nasion and glabella, bifrontal and outer biorbital breadths. These features discriminate between flat frontals with large transverse diameters across the supraorbital area (‘archaic’) and curved frontals with small transverse diameters across the supraorbital area (‘modern’). As in Sládek *et al.* (2002), Skhul V and Qafzeh 6, as well as Zuttiyeh, were better associated with the ‘archaic’ hominins in general and Neanderthals in particular supporting the view of Corrucini (1990; 1992) that a morphological dichotomy is not seen in the west Asian sample.

The ontogenetic analysis of interlandmark data found that different growth trends between Neanderthal and recent modern humans can be distinguished if several principal components are examined. The differentiation of the growth trends is greatly dictated by the higher projection of the upper face in both adult and juvenile Neanderthals. This result

is consistent with the Tillier (1983; 1986, cited by Tiller 1989) who found that nasal protrusion, a feature that is equivalent to the definition of the projection of the upper face in the presented analysis, develops very early in Neanderthal ontogeny. Ponce de Leon and Zollikofer (2001) reported similar trend in their 3D analysis.

The analysis of inter-landmark distances highlight particularities of the Teshik-Tash morphology. On one hand, it is similar to adult Neanderthals due to its relatively large size and the combination of the relatively flat frontal and wide diameter across the supraorbital region. On the other hand, it has a flatter upper face than both adult and juvenile Neanderthals, and in this respect it falls within the modern human range of variation. In the general picture of the knowledge on the Teshik-Tash morphology (see below) these features are consistent with the view on the lesser expression of the characteristic Neanderthal morphologies in eastern Neanderthals (Jelinek, 1969; Vlcek, 1991). Unlike Teshik-Tash, the Starosel'e child is within the range of variation of the youngest recent modern humans.

Affinities of the North-East Eurasian fossils

Nine fossils from north-east Eurasia were a particular focus of the present study. Some are better known than others. The following discussion is arranged so that the most well-known fossils are dealt with first.

Sungir' 1, 2 and 3

The Sungir' individuals have a good published record on dating, archaeological and palaeoanthropological descriptions. The Sungir' site is located on the left bank of River Klyasma, east outskirts of the city of Vladimir, 192 km North-East from Moscow. The age of the settlement is defined from the position of the cultural layer in the so-called Bryansk soil, connected with the corresponding interstadial of the Valdai Ice Age of Late Pleistocene. One of the first radiocarbon dates, obtained from collagen in reindeer bones at Groningen laboratory gave an absolute age of 24430+/-400 years ago (Gro 5446) and from charcoal, 25500+/-200 years ago (Gro 5425). Subsequently, a number of dates were published by different laboratories that range from 14,600 to 27,460 radiocarbon years BP (Allsworth-Jones, 1986; Anikovich, 1992; Sinitsyn et al., 1997a; Sulerzhitski et al., 2000; Kuzmin et al., 2004). Dolukhanov *et al.* (2001) offer a calibrated date of 29,900 years BP for the site. A.A. Velichko (1993) divide the process of ancient peopling through the Eastern European plain into four periods, which coincide with the periods of landscape development: pre-Bryansk (up to 32,000 years ago), Bryansk (32000–24,000 years ago), the time of maximum temperature fall (23,000–17,000 years ago) and Latest Valdai (16,000–12,000 years ago). The cultural layer of the Sungir' settlement lies in the depth of the Bryansk soil (Bader and Bader, 2000).

Sungir' 1

The first morphological description of Sungir' 1 individual was given by Debets (1967). He believed that the skeleton recovered during excavations in 1956 belonged to an elderly man (50–55 years of age) of a relatively robust body build but tropical body proportions. The

Sungir' 1 finding consists of the complete cranium and mandible, a number of fractured elements of the spine and thorax, clavicles, sacrum, partial innominate bones, fragments of the hand and foot and virtually complete long bones. Debets (1967) included Sungir' 1 in the group of European Late Palaeolithic fossil humans. Bunak (1973; cited by Bunak, 2000) expressed the idea of great morphological polymorphism within the Upper Palaeolithic population and the lack of geographical segregation in racial features. Bunak (1973) suggests that Sungir' 1 possesses a combination of European and some Asian features, such as the low angle of projection of the nasal bones.

Later, Gerasimova (2000a) provided a detailed description of the Sungir' 1 cranium. This study together with a multivariate analysis by Alexeeva (2000), represent the latest view of the position of Sungir' 1 among other Upper Palaeolithic individuals. They agree on the great variability among the latter fossils and the best association of Sungir' 1 with the west European Upper Palaeolithic population.

Khrisanfova (1984; 2000) offered a description and analysis of the post-cranial skeleton of Sungir' 1. She noted the high stature of the man that was partly due to the relative elongation of the distal limb segments. She also pointed out the very wide shoulders compared to the width of pelvis in Sungir' 1. According to this author, Sungir' 1 possesses an unbalanced combination of features. For example, his clavicles are very long but relatively gracile, as are his arm bones. The long and relatively gracile clavicles are known for Neanderthals but, according to Khrisanfova (2000), Sungir' 1 has even thinner clavicles for their length. In contrast, his femora are very robust (i.e. have large diameters relative to their length and robust epiphyses). Similar dissociation is found in proportions of hand and foot bones. A number of features of the Sungir' 1 postcrania, such as long limbs and high

stature as well as low curvature of its long bones, align it with tropically proportioned people from Skhul and Qafzeh, especially with Skhul 4 and early Upper Palaeolithic individuals from Europe. However, the proportions of the upper to the lower girdle, the length of the clavicle compared to its gracility, a number of features of long bone epiphyses and torsion angles of diaphyses, some features of the shape of carpals, metatarsal and tarsal bones are more similar to the Neanderthal state than either to modern humans or to west Asian 'pre-sapiences' (Khrisanfova, 1984; 2000)(Khrisanfova, 1984, 2000).

The present work benefits from the comparison of Sungir' 1 frontal bone not only with the other Upper Palaeolithic individuals, as has been done by the majority of the authors cited above, but also with recent modern humans, as well as representatives of west Asian early modern humans. It has been found that Sungir' 1 frontal, in fact, aligns better with the recent modern human morphology than with any other Upper Palaeolithic individuals in the comparative sample. In the discriminant analysis of the complete frontal bone (Fig.5.13), it falls at the overlap boundary of the 95% distribution of the Upper Palaeolithic group with the recent modern human distribution. According the results of the discriminant analysis, Abri Pataud is the closest Upper Palaeolithic individual to Sungir' 1. However, the consensus shape of the Australian population has the absolutely smallest Procrustes distance with Sungir' 1 frontal (0.0018), and with Teita consensus shape being the next closest (0.0021). The range of distances in recent modern human populations goes up to 0.0076 for Buryats, whereas the range of Procrustes distances in fossils range from 0.0056 for Mladeč 5 to 0.0256 for Broken Hill.

The proximity of Sungir' 1 frontal to the recent modern human morphology underlines the variety in the Upper Palaeolithic modern humans. It may also create grounds for the

argument that some of the fossil modern humans (such as Sungir' and Abri Pataud) dated to around 22,000–23,000 radiocarbon years BP were closer to the non-European source of the recent modern human variation than to the earlier individuals from the European Upper Palaeolithic. This conclusion points suggest two or more events in colonisation and re-settlement of Europe before and during the last glaciation as suggested by recent analyses of mitochondrial DNA and its coordination with the archaeological data (see summary in Forster, 2004; as well as detailed presentation of genetic research in Richards et al., 2000; Torroni et al., 2001; Loogvali et al., 2004; Pereira et al., 2005).

Sungir' 2 and 3

Analyses of dental and postcranial morphology as well as genetic analysis provide for suggestions on the age and sex of the virtually complete skeletons of Sungir' 2 and Sungir' 3 children (Mednikova et al., 2000; Zubov, 2000; Poltoraus et al., 2000) Sungir' 2 most possibly belongs to a boy of 11–13 years old and Sungir' 3 is a girl of 9–10 years of age. Trofimova (1984) offered the first detailed anatomical description of Sungir' 2 and 3 crania. She found that Sungir' children had generally larger skulls than modern children of the same dental age and possessed a mosaic of morphological features some of which she considered similar to Předmostí 22, an Upper Palaeolithic child of about 9–10 years (Trofimova 1984) and some, such as the presence of a slight occipital bun in both children, height of the temporal bone and absolute values of facial diameters, to the Neanderthal child from Teshik-Tash. A subsequent publication by Gerasimova (2000b) revises the Neanderthal features of the Sungir' children and argues for the lack of ground for such identification. She notes, for instance, that the occipital bone of the Sungir' 2 boy has been reconstructed from eight pieces. The *sulcus praenasalis* listed by Trofimova (1984) as a

Neanderthal feature in Sungir' 2, was also partly reconstructed and actually has an intermediate shape between such found in Neanderthals and modern humans (Gerasimova, 2000b). The relative height of the temporal bone to its width and width to its height in Sungir' 2, in fact, fall within the modern human variation and differ from Neanderthals. Nevertheless, Zubov (2000) has found a number of 'archaic' characteristics in the structure of otherwise modern teeth of the Sungir' children. These are macrodontism of incisors and canines (large values of vestibulolingual diameters that exceed variation in the Upper Palaeolithic, and are even larger than in some Neanderthals), the median ridge on the lingual surface of the upper incisors (whereas no shovel-shape is registered), reduction of the upper molars metacone with large hypocone, rounded crown shape of the lower molars, molarisation of the second lower premolars, and additional elements of the third level on the molar masticatory surface.

Nikituk and Kharitonov (2000) describe the postcranial remains of Sungir' 2 and 3 children. One of the major conclusions from this work is the similarity of proportions of Sungir' children with the Sungir' 1 adult male, especially noticeable in relatively long and gracile clavicles, translated into the relatively wider shoulders of both children, in combination with the high robusticity of their long bones.

The analysis of the frontal bone shape has firmly placed both children within the range of recent modern sub-adults. Given that no other Upper Palaeolithic sub-adults were available for comparison in the present work, it is not possible to judge whether Upper Palaeolithic children in general would demonstrate a different growth pattern from one in recent modern humans. In any case, neither the Sungir' 2 nor the Sungir' 3 frontal shows a particular similarity to Teshik-Tash (Fig 4.22a). On the contrary, all Sungir' individuals have a

relatively close position along the ‘archaic’ relative warps in both complete frontal bone and supraorbital region analyses (Fig.5.23b).

The younger girl, Sungir’ 3, is found to be slightly more similar to adult modern individuals than is the older boy, Sungir’ 2 (Fig.5.22a and 4.23a). Sungir’ 3 and Sungir’ 1 fall in the middle of recent modern human variation along the second, ‘archaic’, relative warp in the analysis of the complete frontal (Fig 4.23b). In contrast, Sungir’ 2 is better associated with the Upper Palaeolithic group in the comparative sample.

In sum, Sungir’ 2 and 3 do not demonstrate any Upper Palaeolithic features in frontal bone morphology, and they fit within the recent modern human range of variation. There is a better association of the Sungir’ 2 boy with Upper Palaeolithic individuals in the sample, which is consistent with the Upper Palaeolithic origin of the Sungir’ population. It is interesting to see that the Sungir’ 3 girl of estimated 9–10 years of age is more advanced in frontal bone development than the 11–13 year old boy, which may be due to the acclaimed faster development in girls of pre-pubertal age.

Teshik-Tash

Hominin remains were recovered during the excavations of 1938 by A.P. Okladnikov in the Teshik-Tash grotto, Gissar mountain range, south Uzbekistan. The grotto contained up to five cultural layers bearing Mousterian artefacts. The remains were found underneath the first, upper cultural level (Okladnikov, 1949). The authors of the excavation claimed that the human remains were found near a fire hearth contained in this cultural level. The skull was squashed by the overlying matter into many pieces, which, however, were lying close to each other. It was also suggested that the loss of the majority of the child’s body parts

was due to the activity of carnivores after the burial when the grotto was left by people for good. The preliminary suggestion of Middle Palaeolithic age of the site was based on the Mousterian type of cultural artefacts and the archaic look of the human remains. The fauna was found to be similar to the present-day one and therefore not useful for dating purposes. However, Gromova (1949) put forward a hypothesis that the occupation of the grotto must have occurred during one of the latest glacial interstadials (most possibly Mindel-Riss), when the climate of Central Asia was similar to the present day. During the 2-year excavations in 1938–1939, the whole grotto was cleaned out and all cultural levels removed.

As mentioned above, the Teshik-Tash hominin find consists of a virtually complete skull, which, however, was reconstructed from as many as about 150 pieces by M.M. Gerasimov, an almost complete mandible and a number of postcranial elements. The postcranial remains include fragments of vertebrae (including a complete atlas), clavicles (left one is complete), fragments of ribs, fragment of an ischium, diaphysis of both femora, fragments of diaphysis of tibia, diaphysis of the left humerus and a number of unidentifiable fragments (Sinelnikov and Gremyatski, 1949; Gremyatski, 1949).

Apparently, there was very little doubt about the Neanderthal affinities of the Teshik-Tash hominin at the time of its discovery. Gremyatski (1949) provides for a detailed comparative analysis of the cranial remains. He concludes that the dental age of the child is equivalent to 8–9 years of age of modern European children. However, he notes the relatively greater size of the Teshik-Tash neurocranium and taller face compared with the modern children of the same age. He hence hypothesises on the faster rate of growth in Neanderthal children, especially in the neurocranium. He suggests that by the age of 8–9, Teshik-Tash has almost

reached adult neurocranial size and was at the stage of the rapid catch-up growth in its facial skeleton. The above author points to a number of archaic (or 'pithecoïd') features in the Teshik-Tash cranium and mandible, such as lack of the mental eminence, very high face, large teeth, absence of the canine fossae, the initial development of a prominent browridge, small mastoid processes and a low, posteriorly prominent occipital.

According to Gremyatski (1949), the general shape of the skull is similar to La Quina 18, a Neanderthal child 1.5–2 years younger than Teshik-Tash. The following description of the Teshik-Tash cranium is derived from the work by Gremyatski (1949) unless stated otherwise. The Teshik-Tash cranium is relatively taller and the frontal bone is more curved than in adult Neanderthals but still flatter than in modern children. The distinctive Neanderthal features include a clear presence of the occipital bun. The occipital bone in Teshik-Tash is hence highly curved and wide rather than tall. The squama of the temporal bone is quite low. The frontal bone is relatively low and wide, no frontal eminences are noticeable. The supraorbital ridge is already well outlined. It is merged at glabella and goes up to the zygomatic processes of the frontal bone where it slightly thins out. According to Gremyatski (1949), the development of the ridge is not yet extended to the upper orbital rims which are still relatively sharp. Orbits are relatively high and almost oval in shape. Zygomatic bones and maxilla are partly damaged but still impress by the relatively flat surface and slightly 'swept back' profile of the first and the large size of the second. The base of the skull is noted to have relatively low flexion "...opistion, basion and infradentale lie almost on one straight line" (Gremyatski, p. 159, in Russian). The foramen magnum is slightly damaged but with some minimal reconstruction gives a good estimate of the real size, which is very large compared with modern children, and is oval in shape. The position

of the foramen magnum is slightly shifted backwards in relation to the line between external auditory meatae. Gremyatski (1949) also notes that the mandibular fossa is relatively flat and not very wide. However, the longer diameters of the fossae are positioned almost transversely, as was also noted for other Neanderthals (Gremyatski, 1949). The palate of Teshik-Tash is larger than in modern children of the same age. The mandible is also very large. It is especially noticeable in the posterior part of the mandibular body which is elongated behind the first deciduous molar and has a wider ramus. There is space posterior to the M1 of the mandible where one can observe the first signs of the M2 emerging into occlusion that makes it difficult to judge the presence or absence of the retromolar space (personal observation). As mentioned above, there is no mental eminence. Gonial angles are truncated but to a lesser extent than in adult Neanderthals. However, Gremyatski (1949) notes that mental foramina are positioned between p1 and p2 (or, in reality, under the deciduous m2s, which are still in place, personal observation). The inferior body of the mandible is inflated so that the insertions of the digastric muscles are shifted to the inferior plane of the mandibular body. In the discussion of the internal surface of the mandible, Gremyatski (1949) mentions that genioglossus and geniohyoid muscles most possibly inserted into the genial pit, rather than attach to genial tubercles as in modern humans. However, another important Neanderthal feature, the mylohyoid bridge (Creed-Miles et al., 1996) is not present in Teshik-Tash (personal observation), whose mandibular foramina display lingulas and a distinctive mylohyoid groove. Among many specific features of the Teshik-Tash dental system, Gremyatski (1949) lists the mild taurodontism of the teeth and the shovel shape of the upper medial incisors.

From comparisons with the literature, it is easy to see, that the Teshik-Tash child displays some derived Neanderthal features, such as the occipital bun, size and shape of the foramen magnum, taurodontism and the shovel shape of the upper incisors, together with such plesiomorphic Neanderthal features as absence of the chin and supraorbital ridge. Some of the Neanderthal features, such as the 'en-bombe' shape of the neurocranium, are expressed to a lesser extent than in other Neanderthals, perhaps due to the young age of the Teshik-Tash child. However, some other features, such as the position of the mental foramina and lingula of the mandibular foramen, are more characteristic of modern humans than Neanderthals. These features allowed speculation on non-Neanderthal affinities of Teshik-Tash. Thus, Weidenreich (1945) saw a connection between Teshik-Tash and the Mount Carmel hominins, such as Skhul and Qafzeh. This opinion has been debated in Russian literature (see, for example, Debets, 1947) and culminated in the work by Gremyatski (1949) cited above where Teshik-Tash was concluded to be a Neanderthal.

However, the doubt in the Neanderthal status of Teshik-Tash has not completely disappeared. For instance, Ritzman (2005) and Glantz and Ritzman (2004) argued that multivariate statistical analysis of the Teshik-Tash cranium places it outside the Neanderthal variation but associates it with modern humans. This opinion feeds into the discussion on who was making the Mousterian artefacts in Central Asia (Glanz *et al.*, in press). The recent work on hominin remains from Obi-Rakhmat and Anguilac grottos by Glantz *et al.* (2003; 2004; in press) as well as a new description of hominin remains from Okladnikov cave (Viola *et al.*, 2006) stress the difficulty of classification of the Central Asian findings partly due to the fragmentary nature of the remains as well as to the simple absence of diagnostic Neanderthal features in the available material. This research revives

the opinion by Weidenreich (1945) on the possibility of early modern human migrations from Levant and Central Asia that would not contradict the Middle Palaeolithic character of the culture associated with human remains since Skhul and Qafzeh hominins are thought to produce the same kind of lithic artefacts.

It is hardly disputable that the on-going work on the direct dating and DNA extraction from Teshik-Tash bone tissue will shed more light on the problem of the eastern boundary of Neanderthal dispersion (B. Viola, personal communication). However, within the modest limits of the present work, it is possible to note that the Teshik-Tash frontal bone morphology fits along the Neanderthal ontogenetic growth trajectory but deviates towards the non-Neanderthal west Asian Late Pleistocene fossils and, ultimately, Upper Palaeolithic modern humans. The features of the Teshik-Tash frontal bone morphology include its large size, close to the adult Neanderthals and modern humans that is in contrast with the shape of the Teshik-Tash frontal that is closer to the very youngest Neanderthals (or the most robust Upper Palaeolithic modern humans) in comparative samples. Teshik-Tash was also found to have a flatter upper face than West European juvenile Neanderthals. This observation is in agreement with the conclusions by Vlček (1991) and Jélinek (1969) on the relatively lesser degree of expression of the Neanderthal autapomorphies in the eastern Neanderthals that include the Teshik-Tash fossil.

Unfortunately, it was not possible to include any sub-adult fossils from Skhul and Qafzeh into the present analysis and hence no definitive conclusion on the similarity of Teshik-Tash to this group can be offered. Nevertheless, if one takes into account results by Ponce de Leon and Zollikofer (2001), who included some of the west Asian sub-adults in their analysis, it is unlikely that the Neanderthal classification of Teshik-Tash might be altered

by geometric morphometric studies of its cranium. In my opinion, the most parsimonious conclusion is to consider Teshik-Tash a Neanderthal. It demonstrates variation within Neanderthals, variation that is already implied by including west Asian specimens in the Neanderthal species.

Starosel'e

The history of the Starosel'e child is arguably the most eventful out of all the fossils from the former Soviet Union. Discovered in 1953, it has received a lot of specialist attention from the first day of its recovery from a Middle Palaeolithic cultural level at a cave site at Starosel'e, Kanley-Dere Gorge, Crimea (see, for example, Alexeeva, 1997 on the history of the discovery). A number of Middle Palaeolithic sites had already been known from Crimea by the time of the Starosel'e discovery, and one of them, Kiik-Koba, had yielded Neanderthal remains (Bonch-Osmolovski, 1940). More Neanderthal remains were recovered from the Middle Palaeolithic site of Zaskal'naya during excavations in 1970, and 1972–1973 (Koloso et al., 1975).

According to the summary of events given by Alexeeva (1997), at the moment of discovery, the association of Starosel'e child with the Middle Palaeolithic level was confirmed by a committee of several professional archaeologists and geologists and all subsequent events on its interpretation followed this conclusion. Very partial remains of a second individual, an adult, were also unearthed from the same level as the child, but it was the virtually complete skeleton of the child that caught the main attention of the scholars. First of all, the modernity of the Starosel'e child made it different from the other Crimean site of Kiik-Koba where Middle Palaeolithic industry was associated with quite archaic-

looking, most possibly Neanderthal postcranial remains. However, by the time of the Starosel'e discovery, a similar situation of association of modern humans and Middle Palaeolithic technology has already been described by McCown and Keith (1939) for Mount Carmel. The Starosel'e case provided a new example of the same story and therefore was initially compared with Skhul 1 infant skull in the first description of Starosel'e by Roginski (1954). The age of Starosel'e child was then determined as about 18–19 months. The following features were noted among 'archaic' on the skull: large teeth, a considerable thickness of the zygomatic processes of the frontal bone and the great width of the anterior section of the mandible (Alexeev, 1976). An argument followed in both Russian and international literature on whether Starosel'e is a Neanderthal, a 'transitional' form or a modern human (Yakimov, 1954; Ullrich, 1955; 1958; Vallois, 1955; Debets, 1956; Bunak, 1956; Gross, 1956; Howell, 1958; Thoma, 1962; 1971; Coon, 1962; Jelínek, 1969; Alexeev, 1976). Notwithstanding the variety of interpretation, the prevailing opinion held Starosel'e child to be a modern individual, morphologically associated either with the Skhul-Qafzeh hominins or with Upper Palaeolithic humans from eastern and central Europe.

The modern status of Starosel'e child put it well in the centre of the dispute on the evolution of modern humans in Europe and Asia. Studies by Ullrich (1955) and Vallois (1955) suggested that the mixture of Neanderthal and modern traits placed Starosel'e child apart from Neanderthals but close to the Skhul hominins. Vallois (1955) proposed that the transition to modern humans did not happen in Europe thus bypassing the 'classical' Neanderthals but rather involved the pool of Mousterian hominins of transitional morphology, such as Skhul-Qafzeh, Starosel'e and Teshik-Tash. Many subsequent studies

employed the association of Starosel'e child with Mousterian technology as an example of the first penetration of early modern humans into areas beyond Levant (Bräuer, 1984; Stringer and Gamble, 1993).

The majority of the studies cited above assumed the correct association of the child remains with the Middle Palaeolithic layer at Starosel'e. However, a serious blow came from Marks *et al.* (1997) who reported on new excavations in Starosel'e. They demonstrated that the initial interpretation of the stratigraphic layers in the site by its first excavators (Formosov, 1958) was most possibly flawed. Moreover, they had discovered two other burials in the vicinity of the Starosel'e child. One of them, a complete skeleton of a middle-aged adult, was an obvious intrusive burial into the same layer where the child was found in 1952. The disturbed ground above it clearly marked a burial pit. The position of the body was identical to the one which was described for the Starosel'e child (extended anatomical position of the body head westwards, face turned to south, pelvis flat on the ground, hands extended along the body, one hand is placed on pelvis). The fragmentary remains of another child were found protruding from a profile partially excavated in the 1950s. This child was found in the uppermost, modern, sediments. Marks *et al.* (1997) suggest therefore that the first finding of the child from Starosel'e should, in fact, be associated with these 18th century Muslim burials stressing the unlikely event of finding two almost identically positioned burials in the near vicinity of each other, one of which would be dated 40,000 years BP and the other 200 years ago.

In summary, it appears quite plausible that the child found at Starosel'e shelter in 1953 is a modern human. However, Marks *et al.* (1997) seem to have altered the outline of a few facts related to the discovery of the child, which was pointed out by Alexeeva *et al.* (1997).

Moreover, Marks *et al.* (1997) themselves refer to the first reports on the child's discovery that point to the absence of the burial pit above the child remains. The latter fact seems to have brought about the firm belief of the Mousterian origin of the child in 1953. Therefore, an additional reference to the child's morphology is useful for further evaluation of the recent claims.

According to the present results, the frontal bone of the Starosel'e child fits well within the variation among modern children along the growth component. This fact, by itself, does not prove the Middle Age date of the child, but it provides some evidence against its Mousterian origin. Traits such as 'thickening of zygomatic processes of the frontal', described as archaic by Roginski (1954), does not translate into similarities between Starosel'e and Neanderthal children in the sample used here. As with Teshik-Tash, the addition of west Asian early modern human sub-adults into the comparative sample may change the position of Starosel'e. However, taking into account the possibility of incorrect dating, it is reasonable to take a cautious position and exclude Starosel'e child from the early modern human paradigm until its Middle Palaeolithic origin is confirmed.

Summarising implications for the two fossils from the southernmost borders of the former Soviet Union, one can conclude that, there is as yet no clear evidence for an association of early modern humans with Middle Palaeolithic artefacts in this territory. Given that Starosel'e is omitted from the early modern human group, the remaining fossils include Zaskal'naya and Kiik-Koba from Crimea, Mesmaiskaya and Barakay from the North Caucasus and Teshik-Tash, Obi-Rachmat, Anguilak and Okladnikov cave from Central Asia. Some of these remains are confirmed Neanderthals, such as the Mesmaiskaya child by DNA (Ovchinnikov *et al.*, 2000) and Kiik-Koba and Teshik-Tash by morphologies that

fit within the variation of Neanderthals. Other specimens are reported to demonstrate 'archaic' traits but not conclusive enough to include them either into Neanderthals or early modern humans. Further analysis is required to resolve this dilemma.

Satanay

The Satanay calvarium was found in the course of excavations in the Gubski Shelter No. 7, Gubski Gorge, North West Caucasus, in 1975 (Autlev and Lubin, 1994). The site is dated as Late Pleistocene and yielded a large collection of Upper Palaeolithic artefacts (15,568 objects), including Gravettian points and bone tools (same authors). The human remains were found in the north-west corner of the shelter in a disturbed burial. Other human remains from the site included a humerus fragment, mandible, femur, a fragment of a tibia, phalanges and fragments of ribs.

Studies of the Satanay human calvarium and fragmentary postcrania have so far only been published in the Russian literature. Preserved parts of the skull include the frontal bone, two zygomatic bones, temporal bones (mostly squamal parts) and the occipital squama (Fig 2.4). Maxilla and basicranium are almost totally missing. The first morphological description of the calvarium is by Romanova and Kharitonov (Romanova and Kharitonov, 1984). The calvarium has been reconstructed from adjoining parts by G.P. Romanova. The authors of the first description noted the narrow and low outline of the neurocranial vault of Satanay calvarium with an especially flat frontal bone. Its supraorbital relief is very well developed and projects forward from underneath the calvarium in the superior view. The age and sex of the specimen have been the subject of disagreement. Notwithstanding the supraorbital relief, the object is relatively gracile, so that it was initially thought to belong

to a female. However, further metric comparison caused Romanova and Kharitonov (1984) to assign it to a male individual. Kharitonov (personal communication) has also suggested that the Satanay calvarium could have belonged to a relatively young male, hence its gracility.

The authors of the first description find the Satanay calvarium dolichocranic, more similar to the central European Upper Palaeolithic than to the west European fossil humans (Romanova and Kharitonov, 1984). In particular, they mention that the sagittal outline of the frontal is similar to Předmostí III and IV, whereas the development of the supraorbital relief is similar to Oberkassel, Mladeč V and VI, Pavlov and Sungir' 1. By its metric characteristics, Satanay calvarium was found to be the closest to Kostenki II and Kostenki XIV (Romanova and Kharitonov, 1984).

My personal observations of the cranium confirm the pronounced supraorbital relief, flatness of the frontal and dolichocranic shape of the neurocranium. The supraorbital relief is clearly divided into superciliary arches and supraorbital trigones due to the thinning of the central portions of the relief to the lateral of the supraorbital notches. However, the lateral supraorbital margins are rounded, merged with supraorbital trigones and protruding from underneath the frontal squama.

In the analysis of inter-landmark distances, Satanay is more similar to Neanderthals than any of the other North-East Eurasian fossils apart from Teshik-Tash. In particular, it was found to be very similar to the Šal'a frontal bone in general dimensions and the value of its frontal angles (from nasion and from glabella). However, the 3D analysis did not confirm this result. Although Satanay differs from the majority of modern humans by its flat and

narrow frontal bone (especially in the middle portion of the frontal squama, with slightly more developed supraorbital relief), the combination of shape features of Satanay is different from that found in 'archaic' hominins, including Neanderthals. In fact, the relative length of the frontal squama and relatively narrow temporal fossae in Satanay as found in the analysis of the complete frontal bone (Fig.5.12) are similar to that in many recent modern humans. This combination is different from the relatively flat but short frontal bones and expanded temporal regions in Neanderthals and other archaic hominins in the analysis who also have expanded more inflated lateral portions of the supraorbital ridge.

The discriminant analysis of the complete frontal bone shape and of the supraorbital relief found Satanay to be intermediate between modern humans and Neanderthals suggesting a mix of affinities. Local variations in the Upper Palaeolithic population may offer a suitable explanation for the peculiarities of the Satanay morphology. For example, it is close to Skhodnya and Khvalynsk in two of the three dimensions in Multidimensional scaling analysis for the complete frontal bone (Fig.5.14). However, Satanay demonstrates no similarity to the geographically closest North Caucasian calvarium from Podkumok.

Khvalynsk

The Khvalynsk fragment was found in 1927 and soon entered literature as a 'Neanderthaloid' or an eastern Neanderthal form (Weinert, 1932; Eikstedt, 1934). The full description in Russian has been published by Gremyatski (1952a). The Khvalynsk calvarium was found in river alluvium, which, according to Bader (1940; 1952b), represents one of the oldest and lowest alluvial levels of the Volga river in its lower stream. At the place of the discovery on Khoroshevskiy Island near Khvalynsk, this level contained

mammoth faunal assemblage. The Khvalynsk fragment was imbedded in this pebble alluvial horizon when discovered. It also had a similar level of fossilisation and brown colour as the faunal remains from the same level. Later, in 1939, a human femur fragment, which had similar fossilisation level and colour, was found at the same place. Nowadays, it is not possible to re-visit either Khoroshevskiy Island or any other fossil-containing banks in this part of the Volga River due to their flooding in the process of creation of Saratov 'Hydro-Electro-Station' and Saratov water reservoir. Therefore, direct dating may be the only option left to uncover the age of the Khvalynsk fragment.

The Khvalynsk calvarium represents a fairly complete frontal bone joined with anterior fragments of two parietals. Both temporal areas of the frontal are broken off below the temporal lines. On the right side, about two thirds of the temporal fossa is still in place, whereas on the left side it is almost totally absent. The zygomatic process and about half of the lateral portion of the supraorbital margin are preserved on the right side. Medially, the break almost totally reveals the right frontal sinus, which is opened up almost to the glabella. On the left side, the supraorbital margin is intact with the exception of its medial portion, where the inferior break opens into the left frontal sinus. Notwithstanding the damage to the naso-glabellar area, there is a short stretch of the fronto-nasal suture preserved between the left maxillofrontale and the nasion. The glabellar part is intact on the left side so that the glabella point itself is not lost. Only short anterior stretches of the orbital plates are preserved adjacent to the intact parts of the supraorbital margin. Neither medial sides of the orbital walls nor ethmoidal cells are preserved. Most of the posterior structures of the nasal area are also lost. In general, the bone is relatively thin and gracile.

In his description of the bone, Gremyatski (1952a) disagreed with the earlier claims on the Neanderthal affinity of the Khvalynsk calvarium but noted a 'combination of modern and Neanderthal features' in the cranium. Among the latter he mentions the flatness of the frontal, relatively well developed supraorbital relief, the relationship between the sagittal length of the supraorbital and neurocranial parts of the frontal (with the former being considerably longer than in modern humans and closer to the size in Neanderthals), the relationship between interorbital and outer biorbital breadth and a low bregmatic height of the object. The latter size was reconstructed by Gremyatski (1952a) by the orientation of the fragment in relation to the position of the zygomatic processes of the frontal and is generally meant to demonstrate the low height of the neurocranium.

In total, the Khvalynsk fragment gives an impression of gracility due to its thin bone and relatively small size. However, it has relatively flat frontal squama and prominent supraorbital relief. The latter has protruding glabella and rounded supraorbital margins which are merged with the supraorbital trigones of the bone. The supraorbital relief thins out laterally but the separation between the medial and lateral portions of the supraorbital ridge is not obvious, perhaps due to the damage to the face of the superciliary arches. One feature that was not mentioned by Gremyatski (1952a) is the relatively short sagittal diameter of the frontal compared with its width.

Multivariate analysis of inter-landmark distances of the Khvalynsk frontal did not reveal any particular affinities with archaic hominins in the comparative sample. The 3D analysis, however, brought about slightly different results. In the relative warp analysis of the complete frontal, Khvalynsk was found to fringe modern human variation at the border with the archaic hominins in the comparative sample (Fig.5.2) together with Předmostí 3,

Cro-Magnon 2, Maldeč 5 and Skhodnya. Some particular features of the Khvalynsk frontal were revealed by the fourth relative warp in the analysis of the complete frontal. They are the elevated flatness of the frontal in combination with the narrow temporal fossa and relatively larger development of the supraorbital relief. In these traits, Khvalynsk is similar to Skhodnya and Skhul V. In addition, the listed characters are correlated with cranio-caudally narrower supraorbital region, straighter outline of the supraorbital margins in the frontal view and longer coronal suture with relatively posterior position of bregma that creates a triangular outline of the posterior squamal border in opposition to the shorter and rounded outline of the coronal suture in the majority of individuals of the comparative sample. From the classification by the Discriminant function, Khvalynsk has been assigned to Neanderthals. This classification has been quite difficult to predict given that this fragment lacks such Neanderthal features as the double-arched, equally developed browridge. In general, Khvalynsk is very similar in shape to Skhodnya and clusters with it in both the Relative warp analysis and in the Multidimensional scaling for the complete frontal bone.

In supraorbital relief, Khvalynsk falls outside the variation in recent modern humans along the second relative warp, which differentiates between modern and 'archaic' hominins together with such west Asian fossils as Qafzeh 6, Shanidar and Zuttiyeh. This result is particularly interesting given that the Khvalynsk frontal is considerably less robust than either of these forms. This result is supported by the Discriminant analysis where Khvalynsk has been assigned to the Neanderthals. The Multidimensional scaling of the supraorbital region has also placed Khvalynsk relatively close to the Neanderthals, away from modern humans.

In summary, the results of the complete frontal bone analysis are quite ambiguous in placing it within the boundary of recent modern human variation along the 'archaic' component but failing to classify it as a modern human in the Discriminant analysis of the 90% of variation in the sample. The shape of the supraorbital relief in Khvalynsk is similar to such west Asian hominins as Qafzeh 6, Shanidar and Zuttiyeh. However, the relative warp analysis of the supraorbital relief alone generally provided less power of discrimination between different groups of Late Pleistocene fossils. The combination of the 90% of variation in the Discriminant analysis placed Khvalynsk within the Neanderthal group. The combination of the morphological features of the frontal in Khvalynsk makes it difficult to unambiguously assign it either to one of the modern human groups in the sample or to Neanderthals. It obviously shows close similarity with Skhodnya, and, to a lesser extent, with west Asian Late Pleistocene hominins as well as with Neanderthals in the shape of the frontal bone.

Skhodnya

A human calvarium was discovered during construction work in the left bank of the Skhodnya River (close to the north-west border of Moscow, Russia) in 1936. The stratigraphical position of the find has been analysed by Sakharov (1952) and Bader (1952a). The calvarium was embedded in sands of the alluvial terrace of the River Skhodnya, on top of an ancient landslide that was later buried by these alluvial deposits. Bader (1952a) suggested that the geological history of the region and the finding of periglacial faunal remains in the layers above the position of the calvarium justify its dating as the last stages of the Last Glacial Maximum.

Three features of the Skhodnya calvarium caused great interest in the scientific community at the time of its discovery. First of all, the bone was found to be significantly fossilised, and the level of fossilisation was determined to be greater than for the faunal remains from the layers above the calvarium. Second, the morphology of the calvarium was noted to be markedly different from modern humans mostly due to the flatness of the frontal squama and the relatively high development of the supraorbital relief. And finally, the surface of the calvarium showed a clear imprint of a fabric on it. The general opinion on the origin of the calvarium settled on its late Upper Palaeolithic association (Bader, 1952a; Gremyatski, 1952b).

In his morphological analysis of the Skhodnya calvarium, Gremyatski (1952b) points out several features that, in his opinion, place it between modern humans and neanderthaloid forms of central and eastern Europe. These features include flatness of the frontal, higher development of the supraorbital relief than is found in modern humans, and large frontal sinuses confined to the supraorbital relief. However, Gremyatski (1952b) noted that the supraorbital relief did not form a characteristic ridge as in Neanderthals because the superciliary portions of the supraorbital relief in Skhodnya were thinning out laterally.

From my personal observation, it is impossible not to register the high inflation of the superciliary arches of the fragment and the deepening above the glabella so that a 'butterfly' effect is created. The supraorbital relief is clearly separated into superciliary arches and supraorbital trigones (also mentioned by Gremyatski, 1952b). The latter is merged with the supraorbital margin creating a rounded outline.

The fragment preserves most of the frontal and anterior portions of the parietal bones. The temporal fossae of the frontal are mostly lost, but temporal lines are intact. The glabella region has a spherical hole in the centre that does not open into sinuses and has rounded margins. Most probably, this has a pathological origin. The orbital plates are broken off except at their very anterior parts. An opening into the left frontal sinus is exposed at the inferior break of the left medial orbital wall. Zygomatic processes of the frontal are fairly well preserved with some bone chipped off on the left side posteriorly. The fragment is highly mineralised and is of a dark chocolate-brown colour, which is claimed to be the result of high iron content (Gremyatski, 1952b).

In the present analysis, the inter-landmark distances have placed Skhodnya frontal bone within the range of modern human variation, although the position of Skhodnya is not in the centre of the variation but rather closer to the edge of the 95% distribution of the Australian individuals in the analysis (Figs. 5.2). In the 3D analysis of the relative warps and in Multidimensional scaling, Skhodnya is found to be very similar to Khvalynsk in the morphology of the complete frontal bone. It has almost identical loading along the ‘archaic’ relative warp in the analysis of the complete frontal, taking a position between modern humans and ‘archaic’ hominins and is equally singled out along the third and fourth relative warps due to the combination of the flat squama, shallow temporal fossa and elevated development of the supraorbital relief, similar to Skhul V (Fig. 5.10a and 5.11a). In particular, Skhodnya is different from other individuals in the sample and similar to Skhul V due to the shape of its coronal suture and the posterior position of bregma. The Discriminant analysis has found Skhodnya to be an outlier to the three *a priori* groups,

although the first group of classification for Skhodnya is recent modern human, whereas it is Neanderthals for Khvalynsk.

The result of 3D analysis of the supraorbital relief in Skhodnya looks slightly different. The supraorbital relief in Skhodnya is larger than in Khvalynsk, which is reflected in the position of Skhodnya among such hominins as Singa, Amud, Neanderthal and Předmostí 3 along the second relative warp in the analysis of the supraorbital region (Fig.5.17). Also, it neighbours Skhul V, Shanidar, Gibraltar 1 and Singa in the first two dimensions in the Multidimensional scaling (Fig.5.21). Nevertheless, Skhodnya falls outside 95% of the Neanderthal distribution being positioned very close to Qafzeh 6 in the Discriminant analysis of the supraorbital region.

In sum, the Skhodnya calvarium shows a very particular combination of features making it difficult to assign to any of the groups in the analysis. It is rather different from both recent and Upper Palaeolithic modern humans but it also does not associate well with the Neanderthals. It is close to Khvalynsk and Skhul V in the general shape of the frontal, whereas the shape of its supraorbital relief brings it close to west Asian Neanderthals, Qafzeh 6 and Singa. Given this result, the question of the origin of the fabric imprint on the surface of the fragment becomes especially controversial. Bader (1952a) experimentally demonstrated that the positive imprint of the fabric on the surface of the bone must have occurred due to the resorption and weathering of the bone in between the fabric threads.

There is very little evidence of the use of woven fabrics in the Upper Palaeolithic. (Soffer et al., 2000) there is a number of reports of small fragments of fired and unfired clay from Donli Věstonice I, II and Pavlov I that have impressions of woven material on them (Soffer

and Vandiver, 1994; 1997; Soffer et al., 2000; Soffer, 2004; Adovasio et al., 1996; 2001).

Several objects from the Upper Palaeolithic assemblages have also been interpreted as tools associated with textile production: a “spear head” from Předmostí that may be a net spacer, the sitting antapomorphs from Předmostí and their equivalents from Avdeevo (Russia) that could be used as loom weights, “rondellers” from Sungir’ and perforated mammoth-bone discs from Mezhirich that may have served as spindle works, and the foot-shaped pendant from Kniegrotte (Germany) that could be a grass comb (Soffer *et al.*, 2000). In addition, Soffer (2004) demonstrated that wear of the working edges on the bone points from Vogelherd (Germany), Kostenki IV and Avdeevo (Russia), Předmostí and Dolni Věstonice I (Czech Republic) must have resulted from their usage to fashion plant based fibres into more complex constructions. Therefore, the textile imprint on the external surface of Skhodnya could represent another example of weaving in the Upper Palaeolithic, if its antiquity is confirmed by direct dating. The morphology of the bone does not contradict the probability of its old age.

Podkumok

The discovery of the Podkumok calvarium and its geological origin has the most obscure circumstances. It was found during canalisation works in Pyatigorsk, North Caucasus, in 1918, at the brink of the town’s surrender to the White Army forces in the heat of the Civil War in Russia. The fragment was passed to M.A. Gremyatski shortly after its finding, who personally examined the place and later discussed the geological origin of the fossils with V.P. Rentgarten, a geologist who examined the region for a geology committee at that time. Later, Gremyatski (1922) and Rentgarten (1922) published their conclusions on the discovery, assigning it to the ‘late diluvium’, i.e. some point in the Late Pleistocene.

On his examination of the morphology of the fragment, Gremyatski was impressed by the large development of the supraorbital relief of the frontal bone, which "...is set anteriorly to the squama and is differentiated from the neurocranial part of the frontal being solely responsible for the formation of the supraorbital rim" (Gremyatski, 1922, translated from Russian). Gremyastki (1922) does not fail to notice the distinction between superciliary arches and supraorbital trigones on the frontal, but points to the great inflation of the latter, which extends onto the zygomatic processes of the frontal (Fig. 2.1).

Two other features were also mentioned as having similarity with Neanderthals: the supratotal sulcus, especially pronounced in the supraglabellar area, and a low angle of the frontal bone. The latter was reconstructed by Gremyatski by orientation of the frontal bone following recommendations by Schwalbe. He also mentioned a number of other 'primitive', but not diagnostic features: large interorbital width, high interorbital index, insignificant development of the frontal eminences, and presence of the 'crista frontalis', i.e. a shallow sagittal ridge on the frontal above the glabella and the small cranial volume (Gremyatski, 1922). In total, this author attributed the Podkumok fragment to Neanderthals, especially similar to Spy II and Krapina fragments.

The Podkumok calvarium consists of a virtually complete frontal bone joined to two fragments of parietals. The temporal fossae of the frontal have been damaged in their distal parts. The zygomatic processes of the frontal are preserved and show rough articulation surfaces. The supraorbital margin is preserved over the right orbit, whereas over the left, the central and medial parts of the margin are broken off so that the inferior side preserves only the anterior outline of it. The break exposes a large sinus that extends onto the squamal part of the frontal. Only a small lateral part of the left orbital plate is preserved

adjoining the left zygomatic process. The anterior portion of the right orbital plate is preserved along the whole stretch of the right orbit. In the nasal area, the break runs slightly below the naso-frontal suture. Fragments (or a fragment) of nasal bones stay fused with the frontal on the left side of the suture. The position of the nasal bones is skewed to the left creating an impression of a broken and healed root of the nose. The medial walls of the orbital plates are destroyed with the exception of a short anterior fragment on the right side where there is also a fragment of an ethmoidal cell exposed inferiorly.

The bone is very gracile, thin in the squamal part and shows signs of obliteration of the coronal suture that led Gremyatski (1922) to suggest that it belonged to an elderly female. Gremyatski (1922) has also noted the major fossilisation of the bone.

In disagreement with the conclusions by the author of the first description, Podkumok frontal bone does not demonstrate any affiliations with Neanderthals in the present multivariate analysis. Unlike Skhodnya or Khvalynsk, it is always found in association with modern humans and, in particular, with Upper Palaeolithic modern humans of the current comparative sample. The relatively large development of the supraorbital relief in Podkumok does not affect its position. This result is especially interesting given that the only well dated adult Upper Palaeolithic fossil from Russia in the present analysis, Sungir' 1, is better associated with recent modern humans than with other Upper Palaeolithic fossils from Europe.

Summary implications for the North-East Eurasian fossils

The analysis of the nine fossils from north-east Eurasia, although limited to the frontal bone, has uncovered some interesting results. Territorially, these findings cover quite a large region of the former Soviet Union, including Uzbekistan, North Caucasus, Crimea and the Eastern European Plain. In respect of the time, the oldest sites represented in this work are confined to the southern limits of the area: Teshik-Tash in Uzbekistan and Starosel's shelter in Crimea. The Starosel's child has not demonstrated any association with the 'archaic' fossils in the morphology of its frontal bone in agreement with the hypothesis of its Middle-Age Muslim origin (Marks et al., 1997).

Teshik-Tash revealed its close association with the 'archaic' hominins in the sample. It has been shown to fit along the Neanderthal ontogenetic trajectory. However, it has also demonstrated a lower degree of expression of the 'archaic' feature suite than Neanderthal children. In addition, analysis of the inter-landmark distances found that the upper face of Teshik-Tash child is comparatively flatter than that in juvenile west European Neanderthals. This finding generally agrees with the view of Vlček (1991) and Jélinek (1969) on the lower degree of expression of Neanderthal features in eastern Neanderthals, which include the Teshik-Tash fossil.

The above fossils are followed in time by a range of claimed Upper Palaeolithic finds. The only confirmed Upper Palaeolithic humans in the North-East Eurasian sample in this work come from Sungir' on the Eastern European plain. They already associate with recent modern humans in frontal bone morphology in contrast with the majority of the comparative Upper Palaeolithic samples. This finding, if taken together with evidence of

greater similarity of Abri Pataud with recent modern humans, suggests that some of the Upper Palaeolithic humans, dated to 22,000–23,000 radiocarbon years BP, were closer to the modern human morphology than previous generations of modern European settlers and may therefore be representatives of populations that ultimately replaced earlier European migrants during the last glaciation. .

The two fossils from the North Caucasus tell slightly different stories. Satanay is the most recent find among these fossils and its association with an Upper Palaeolithic site is almost certain. From analysis of the 3D data, Satanay was found to be mostly similar to recent modern humans. However, analysis of the inter-landmark data highlighted the combination of the flatness of the frontal squama and the diameter across the supraorbital region, which places this fossil closer to the ‘archaic’ pattern. Podkumok calvarium also comes from the North Caucasus thus being geographically closest to Satanay but has a very poor dating due to the history of its discovery in the 1918. It has been claimed to belong to Upper Palaeolithic times and, in accordance with the present results, also associates well with the Upper Palaeolithic European fossils by the morphology of the frontal. This result makes Podkumok dissimilar from the Satanay frontal and puts it in opposition to the Sungir’ humans who have a more recent morphology of the frontal than other Upper Palaeolithic fossils here.

In addition to Sungir’ fossils, two other finds come from the Russian European Plain: Skhodnya and Khvalynsk. These fossils are, in fact, geographically separated whereby Skhodnya comes from the north-west border of Moscow, whereas Khvalynsk comes from the lower Volga River. Nevertheless, they are found to have certain similarities in the shape of the frontal bone but are different in size (Skhodnya is larger than Khvalynsk). In the

course of the analysis, these fossils have shown both affiliations with modern humans and similarities with ‘archaic’ hominins in the sample. These similarities, on one hand, lie in the ‘archaic’ complex of morphological features of the complete frontal in Skhodnya and Khvalynsk (relatively flat frontal squama, projecting supraorbital relief, relatively wide transverse diameter across the supraorbital region and others) which is found to be at the boundary of the recent modern variation with the dispersal of the ‘archaic’ fossils. On the other hand, the total development and shape of the supraorbital region places them among the ‘archaic’ fossils. These features are counterbalanced by relatively small temporal fossae as well as a longer coronal suture with the relatively more posterior position of bregma than in the majority of other modern and fossil individuals in the sample. As a result, these fossils have a unique combination of features that is difficult to reconcile in comparison with such *a priori* groups as Neanderthals, recent and Upper Palaeolithic modern humans. Skhodnya, Khvalynsk and, to a lesser extent Satanay, do not have evidence for affiliation with any of these three groups. Only reliable direct dating of these fossils will help to understand the reason for the recovered pattern. Given all the information available on the peopling of north-east Eurasia, it is unlikely that either Skhodnya or Khvalynsk would date to earlier than 125,000 years BP: the earliest sites from this region are Elniki II at Kama River, northern Urals, which is dated to probably older than 125,000 years BP, and lower layers at Garchi I (same area), dated to earlier than 60,000 years BP (Pavlov et al., 2004). In respect of Satanay, it is also unlikely to be dated older than the Upper Palaeolithic layers of the Gubski shelter where it was found. However, all three of these fossils can be younger. Given that they are not recent in morphology and do not associate with the Upper Palaeolithic sample from Europe as presented here, they should belong to a third kind of population that has been partly formed under the pressure of geographical differentiation

and genetic drift. Given the geographical proximity of the Sungir' site and the place of discovery of the Skhodnya calvarium, the same Upper Palaeolithic age for both fossils seems unlikely.

The variation presented by Skhodnya, Khvalynsk and Satanay frontal bone morphology does not contradict the hypothesis of multiple dispersals suggested by Lahr (1996).

According to this point of view, multiple dispersals from the ancestral source in Africa and from secondary sources outside Africa gave rise to more than one hierarchical chain of geographical expansions, differentiation by genetic drift, extinctions and new expansions.

In this scenario, at least Skhodnya and Khvalynsk may be contemporaneous, most possibly pre-dating such populations as represented by the Sungir' people. However, the exact course of events to explain the weak association of Skhodnya, Khvalynsk and Satanay with either recent or European Upper Palaeolithic people may be uncovered only by dating of these fossils and subsequent comparison with a wider range of Upper Palaeolithic and Mesolithic populations from Eurasia.

Quantitative reconstruction and its future application

Due to the fragmentary nature of the fossil record, reconstruction and accounting for preservation or damage are an intrinsic part of almost any research on fossils. Its application in palaeoanthropology ranges from the initial assembly of broken parts to speculation on the body-build, locomotion and soft tissues of the extinct hominins (see, for example, Berge and Daynes, 2001). Any reconstruction is based on a set of explicit or implicit assumptions, such as spatial position of cranial fragments relative to each other or

correlations of soft tissue thickness with bony structures. The latest papers on 3D reconstruction of hominin crania by Zollikofer *et al.* (2005) and Gunz (2005) suggest application of clear criteria for reconstruction of missing data whose influence can be statistically verified.

Two assumptions underlie reconstructions in the present work: symmetry of the hominin cranial features and the hypothesis that minimisation of the bending energy of the infinitely thin metal plate can be used for predicting missing points of one shape on the basis of the other. Reconstructions based on both assumptions have demonstrated relatively robust results by yielding shapes similar to the original crania. In the course of analysis it has become clear that the reconstruction of the inter-landmark distances using reflection (the assumption of cranial symmetry) results in unpredictable behaviour of some of the reconstructed individuals. Also, whether the resulting reconstruction will behave similar to the original in the statistical analysis depends on the degree of real-life cranial symmetry of the reconstructed individual and the presence or absence of deformations. The degree of asymmetry in life is unknown. For example, within the presented analysis of inter-landmark distances, individuals such as Skhul V, Tabun, Khvalynsk and Engis demonstrated marked differences from other individuals in the sample in reconstructed diameters and/or angles, which are affected by the reconstruction of the respective diameters. Although these differences may reflect the genuine condition, it is hard to evaluate the extent to which reconstruction has affected the result. Assuming that genuine differences have indeed been just slightly exaggerated in the above four cases, there might be some other cases where reconstruction has masked distinctive morphologies and resulted in a more conservative result.

In contrast to the reconstruction by reflection in the analysis of the inter-landmark distances, the reconstruction with the help of the TPS function was expected to bring about less rather than more differences between the reconstructed fossils and the uniform reference, in other words, bias the result against the hypothesis of individual and group differentiation. Given that the reference shape in this work is the consensus of recent modern humans, an increased similarity of some fossils with recent modern humans could have been the reconstruction side effect. However, the majority of reconstructed individuals clustered well with their respective taxonomic groups (for instance, La Ferrassie, Le Moustier, Gibraltar 1, Gibraltar 2, DV1). In one case did a fossil specimen showed an affinity opposite to the expected effect of the reconstruction (Mladeč 2 resembled Neanderthals in the Multidimensional scaling analysis). Skhul V is another individual that had several areas reconstructed, including a medial portion of the supraorbital relief to the left from glabella and distal portions of zygomatic processes. However, this reconstruction hardly affected the unique combination of features in Skhul V that set it apart from the majority of individuals in the comparative sample. In total, the moderate application of the reconstruction with the help of the TPS function works well for the purposes of the present statistical analysis.

Chapter 7 Summary and conclusions

The major objective of the present work was investigation of the affinities of nine fossils from the territory of the former Soviet Union. They were chosen based on the preservation of frontal bones. Some of these fossils, such as Teshik-Tash, Starosel'e and Sungir' individuals, have previously received detailed morphological and archaeological assessment in the literature. Others, such as Skhodnya, Podkumok, Khvalynsk and Satanay have been mostly known within the Russian speaking palaeoanthropological community, partly due to their poor dating. However, to different extents, all of these fossils have been mentioned in the context of the argument on transition from 'archaic' to modern humans, and Neanderthal affinities have been claimed for some of them.

In order to achieve better understanding of these fossils, a comparative sample of nine recent modern populations (121 individuals, including adults and children) and 44 was analysed. 3D data were collected for anatomically defined landmarks as well as for outlines and surfaces. These data were used in two separate analytical modes. First of all, traditional inter-landmark distances and angles were calculated from the landmark data, and multivariate statistical analysis has been performed for these measurements. Second, semi-landmarks on the outlines and the surface of the frontal bone were generated following a recently developed procedure (Gunz et al., 2005). Then, 71 landmarks and 163 semi-landmarks were used for geometric morphometric analysis of the data.

In the course of the analysis, three questions were a specific focus:

- Is there an explicit pattern of variation of the frontal bone morphology in the sample of adult individuals?
- Is there any pattern in frontal bone variation of the ontogenetic set of data?
- Where do the 'unknown' fossils from the territory of the former Soviet Union (referred to as North-East Eurasian samples throughout the work) fit within the observed pattern?

In general there is good separation between the modern and 'archaic' forms of the frontal, whereby the modern morphology is found in both recent and Upper Palaeolithic modern humans, and the 'archaic' morphology is characteristic of European and west Asian Neanderthals, Skhul V, Qafzeh 6, Zuttiyeh, Broken Hill and Singa. The 'modern' morphology includes a slightly longer, curved squama of the frontal that is relatively wider in its middle portion than across the supraorbital region. The supraorbital region in all 'modern' individuals is taller in the frontal view and relatively flatter in the coronal plane. The superciliary arches are also very small in modern forms. These features almost totally differentiate modern humans from all archaic hominins and are related to modern human autapomorphies of neurocranial globularity and flatness of the supraorbital region. The 'archaic' morphology, on the contrary, is expressed in a relatively flatter (in sagittal projection) and shorter frontal squama, with projecting supraorbital relief that is vertically short and rounded in the horizontal plane, i.e it is sweeping back laterally from glabella. There is also elevation of the supraorbital trigones and a relatively smooth outline of the browridges. The transverse diameter across the supraorbital region is larger relative to the middle portion width of the frontal squama.

As a group, Neanderthals significantly differ from Upper Palaeolithic and modern humans in the morphology of the complete frontal and the supraorbital region in particular.

However, Neanderthals overlap with other archaic individuals in the sample, including such early Anatomically Modern Humans as Singa from Africa and Skhul V and Qafzeh 6 from west Asia. This overlap exists both in the morphology of the complete frontal bone and in the supraorbital relief, but it is more pronounced in the latter, where Neanderthals are also joined by the Upper Palaeolithic fossil Předmostí 3 and North-East Eurasian fossils Skhodnya and Khvalynsk, usually considered Upper Palaeolithic. The Neanderthal browridge morphology is not as distinctive as was expected at the start of the research in the face of variation within the Neanderthals themselves and because of overlap with other archaic hominins in the sample.

In agreement with previous studies, all west Asian fossils have been found to have a less pronounced degree of expression of the 'archaic' features of the frontal bone. With the exception of Qafzeh 1 and 2, which associate with modern humans, all west Asian fossils, including Neanderthals (Amud 1 and Shanidar 1), early Anatomically Modern Humans (Skhul V and Qafzeh 6) and Zuttiyeh cluster relatively close together between the modern humans and some of the classical west European Neanderthals. However, they overlap with the east European fossil from Šal'a, with Neanderthal and with the African early modern human from Singa. This pattern corroborates the views that Neanderthal autopomorphies are less pronounced in eastern Neanderthals. It also shows the lack of a morphological dichotomy in the frontal bone within western Asian Late Pleistocene hominins and, as demonstrated by similarities with the Singa frontal bone, there is possibility of genetic connections between western Asia and Africa.

The Upper Palaeolithic group of individuals represented here differs significantly from the pooled sample of nine recent modern human populations around the world. This difference is partly related to the narrower and more curved squama and greater development of the supraorbital relief in the Upper Palaeolithic individuals. However, given that this analysis included only a limited sample of Upper Palaeolithic modern humans from Central and eastern Europe, it would be wrong to extrapolate this difference to the rest of the world. Nevertheless, this pattern of differentiation is useful for the understanding of mostly eastern European fossil frontal bones.

Recent modern human populations showed considerable overlap in frontal bone morphology throughout the course of the present analysis. However, the possibility of inter-population differences has not been fully explored here due to the relatively small sample of individuals within each population.

The ontogenetic analysis indicated different growth trajectories in recent modern humans and Neanderthals. These trajectories have already diverged by two years of age and they diverge even further as each population approaches adulthood. As a result, adult Neanderthals and recent modern humans differ more in the shape of the frontal bone than do the children of these species.

In the context of these patterns of variation, several conclusions can be made for the North-East Eurasian fossils in the sample.

First, Sungir' individuals (Sungir' 1, 2 and 3) associate with recent modern humans as does the Abri Pataud Upper Palaeolithic human but have only distant affinities with other Upper Palaeolithic fossils in the comparative sample. This conclusion is consistent with the

relatively later dates of Sungir' and Abri Pataud in comparison with the fossils from Dolní Věstonice, Pavlov, Cro-Magnon, Mladeč and Předmostí.

In contrast with the Sungir' individuals that have a definite Upper Palaeolithic date, the poorly dated fossil calvarium from Podkumok showed a very good association with the Upper Palaeolithic group. This may point to the time of origin of the calvarium and if the date is confirmed, demonstrate connections between western Europe and the North Caucasus in the Upper Palaeolithic.

Morphological affinities of three other North-East Eurasian fossils - Satanay, Skhodnya and Khvalynsk - are not easily resolved by classification into one of the three *a priori* groups of Neanderthals, recent modern humans and Upper Palaeolithic modern humans. Each of them is affiliated with recent modern humans or Neanderthals in the discriminant analyses of the 3D data presented here. However, they all fit into the recent modern human distribution in the relative warp analyses, albeit at the archaic end of the spectrum. There is a temptation to affiliate them with the early anatomically modern humans in the sample, such as Skhul V and Qafzeh 6 as has been done by previous authors (Drobyshevski, 2001), but the latter are more distant from the recent modern human morphology than are Satanay, Skhodnya and Khvalynsk. The particular features of these three North-East Eurasian fossils may have local origin. However, they also agree with the hypothesis of multiple dispersals of modern humans from Africa and secondary sources beyond it that were followed by geographical separation and genetic drift (Lahr, 1996). In this scenario, Skhodnya and Khvalynsk might pre-date humans from the geographically close Sungir' site who are characterised by recent morphology of the frontal.

Finally, the frontal bone of the Teshik-Tash juvenile is associated with Neanderthals, which is the most common view of its affinities. However, this association is not definitive, because in some cases, especially in the complete surface morphology of the frontal, Teshik-Tash deviates from Neanderthal infants towards other 'archaic' Late Pleistocene fossils. This pattern agrees with the lesser expression of Neanderthal autapomorphies in eastern Neanderthals.

Acknowledgment

I am most grateful to my supervisors, Leslie Aiello, Charles Lockwood and Mark Collard who have directed me, provided with their just criticism and created opportunities for me at different stages of this project. I am also especially grateful to the Geometric Morphometric team in Vienna, who accepted me among them, provided me with the analytical tools and helped in the course of this analysis: Philipp Gunz, Philipp Mitteroecker, Fred Bookstein, Katrin Schaefer and Gerhard Weber are among them. And of course, all organisations and people who allowed me to work with the original fossil and modern material in their care have my sincere thanks: Vladimir Chtetsov, Vitaliy Kharitonov and Denis Pezhemski from the Anthropology Museum of the Moscow State University; Tatiana Balueva from the Laboratory of Reconstruction, Institute of Anthropology and Ethnology, Russian Academy of science; Robert Kruzinski and Louise Humphrey from the Natural History Museum, London; Phillipe Menecier, Musee de l'Homme, Paris; Maria Teschler-Nicola, the Natural History Museum in Vienna; Maggie Belatti and Martha Lahr, the Leverhulme Centre for Human Evolutionary Studies, Cambridge; Jirí Svoboda, Archaeological Museum in Dolní Věstonice; Alena Sefčáková, Slovenske Narodne Muzeum, Bratislava; Edouard Poty, University of Liege; Michael Schmauder, Rheinisches Landesmuseum, Bonn; and Almut

Hoffmann, Museum für Vor- und Frühgeschichte, Berlin. I would also like to thank a number of people who were just kind and provided their indispensable support in connection with various aspects of my work making my life easier and brighter: Alexandra Buzhilova and Tatiana Alexeeva, Institute of Archaeology, Russian Academy of Science; Isabelle De Groote and Fire Kovarovic, Anthropology Department, University College London. I would like to thank my husband, John Stansfield, for his support and patience in seeing me through this work, without whom it would have never been possible.

Present work has been supported by grants from the University of London Central Research Fund and the Graduate School of the University College London.

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